Matching invasive species to invaded environments using, climate, habitat and phylogeny

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Biological invasions have noticeably accelerated with increases in global trade of commodities, and international travel. While many non-native species cause changes in both managed and natural ecosystems, non-native arthropods in particular, pose a major threat to native biodiversity and economic activity worldwide. To prevent the establishment and impact of invasive organisms, and protect productive and natural ecosystems around the world, risk assessment is necessary. Part of risk assessment is to predict potential establishment of those non-native species that are particularly invasive, and capable of causing considerable economic and/or environmental damage. To accomplish that, knowledge about recipient ecosystem characteristics and the potential invaders that influence invasion success needs to be increased.

Over many decades of study, invasion ecology has provided a number of generalizations about important factors affecting non-native invertebrate and plant species establishment success in newly invaded habitats. Key factors proposed as being important for risk assessment of potential establishment success, of invertebrate arthropods in particular, are propagule pressure, environmental factors, such as climatic suitability, and host availability. However, studies investigating these factors, as well as their consequences, have an important bias towards species of economic interest. That bias exists because economic pests usually attract more scientific attention. The result has been the generalisation that managed ecosystems may be more sensitive to biological invasions than natural ecosystems. Clearly, such a generalisation persists because of the general lack of knowledge and understanding of complex natural ecosystems, and, in particular, the lack of research on non-native arthropod impacts on those systems.

The main aim of this thesis was to carry out research to increase knowledge to help improve risk assessment of the potential establishment and impact of non-native arthropod species that threaten

natural ecosystems, by, 1) compiling records of non-native beetles and spiders established in natural ecosystems in North America, a continental ecosystem, and New Zealand, an oceanic island ecosystem, and comparing their impacts on those ecosystems between the geographic ranges and between the different taxa, 2) determining whether floristic similarity between donor and recipient regions and floristic diversity, are useful complements to climatic similarity for predicting potential establishment, 3) determining if plant host phylogenetic affinities between donor and recipient regions can give useful predictions to evaluate the relative impacts on individual plant species and ecological systems, and, 4) to review different impact classification frameworks available in the literature, and test, using structured expert elicitation methods, if selected frameworks provide better assessments than random attributions of impact levels.

The comparison of the level of impact of non-native beetles and spiders established in the natural ecosystems of North America and New Zealand showed that North American natural ecosystems seem more vulnerable to phytophagous insect invasions than those in New Zealand. New Zealand natural ecosystems, however, appear more sensitive to invertebrate generalist predators, such as spiders. Interestingly, even though there are few species of non-native beetles recorded as feeding on New Zealand native plants, most are also generalist polyphagous species. New Zealand represents an oceanic island ecosystem that is isolated and these results seem to indicate that such an ecosystem might be more invasible by host-generalist invertebrates than a continental ecosystems, such as North America. The relationship between biogeographic origin of the non-native species and their level of impact in each ecosystem, was also studied. But, unexpectedly, there was no clear relationship between the two variables in either ecosystem studied.

As a result of these comparisons and previous work from different authors, the utility of several factors for improving risk assessment of the potential establishment and impact of non-indigenous invertebrate herbivores, further investigated. First, the influence of floristic similarity, floristic diversity and climatic similarity on non-native beetle establishment success was studied. Different models showed that including floristic and climate variables in the same model better predicted non-native beetle presence than models that included the variables separately. However, for the species in this study floristic, similarity between regions in combination with floristic diversity within a region appeared to better explain the presence of non-native beetle species than climate similarity alone.

Another important factor studied in this thesis is whether plant phylogenetic affinities between donor and recipient regions is an important indicator of the establishment success of non-native herbivore species in the recipient region. As expected, the host-range of the non-native herbivore species established in New Zealand are phylogenetically constrained. However, the probability of feeding on

new host plants, and therefore the phytosanitary risk associated with the species, varied among classes of herbivore taxa and among the orders of phytophagous insects. In addition, phylogenetic affinities analysis between potential donor and recipient regions was shown to have predictive power that may allow the identification of potential herbivore pests of native ecosystems as well as which plant genera might be susceptible.

Finally, the initial analysis and comparison of non-native species impacts in different ecosystems, raised questions about how best to assess the impact level and therefore the level of risk in the invaded area. A literature review of different impact assessment tools available to risk assessors showed that there are multiple assessment options; however, most of them are of a qualitative nature which can lead to inconsistencies between assessors. Qualitative frameworks often rank impacts by using statements about important consequences, as severity categories or values determined by the authors, which may increase inconsistency. However, a structured expert elicitation process was used in this study and was shown to increase agreement between the experts using the selected frameworks. Despite the increase in agreement between experts, it is important to note that impact assessments are based on values and not quantities, and as such did not allow accuracy and reliability of the expert opinion to be tested. Clearly developing a generic quantitative framework should be the subject of urgent research.

Overall, this research has contributed to increasing knowledge and awareness of the range of factors that can determine or influence non-native invertebrate arthropod species establishment success and subsequent impact. Specifically, this thesis highlights several factors, particularly floristic similarity and plant phylogenetic affinities analysis, that should be useful additional variables for risk assessors in biosecurity regulatory authorities around the world, to rapidly evaluate the risk of establishment of newly detected invaders. Greater knowledge and more rapid assessments will improve assessor accuracy and efficiency for decisions about management actions for new incursions but also for greater preparedness and prioritisation. Moreover, this research identifies future directions especially for the impact assessment of non-native invertebrate species in natural ecosystems, which will help direct the development of a generic quantitative approach that will ultimately support timely and effective management strategies.

Keywords: non-native species, floristic similarity, climatic similarity, host phylogenetic signal, impact assessment, expert elicitation.

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Chapter 1

General Introduction

1.1 Biological invasions on a global context

Since life first appeared on earth, organisms have colonized new environments by natural dispersal using natural vectors and pathways. However, with human colonization invasive species, especially plants, now dominate landscapes in places such as North and South America and Australia (Williamson, 1999). When analysing the rates of species arrival to oceanic islands, Lockwood et al. (2007) showed that human-assisted immigration rates are quantitatively different from natural immigration rates. For example, Lockwood et al. (2007) calculated that the Hawaiian native flora could have arisen from a natural immigration rate of one species every 100,000 years. However, the actual rate accelerated to one new plant species every 50 years after the arrival of Polynesians, and to one new species every 22 years after the arrival of Europeans. Lockwood et al. (2007) also state that the human-assisted pathways and vectors by which non-native species disperse are much more diverse and variable than natural processes. While it is clear that the transportation and introduction of non-native species to new locations is a pervasive component of human-induced global change (Cassey, 2005) it is important to also recognise many species introduced for agriculture and forestry are beneficial, and many accidentally introduced species have negligible effects (Williamson, 1999).

The total cost of damage and control of non-native species in the United States, British Isles, Australia, Europe, South Africa, India, and Brazil exceeds $300 billion per year (Pimentel 2011). But in addition to the economic costs, species invasions comprise one of the greatest threats to biodiversity, together with habitat destruction (Glowka et al., 1994, cited by Williamson 1999). Non-native species have diverse environmental impacts (Lockwood et al., 2007; Blackburn et al., 2014), which can be classified depending on their effect at various levels of biological organization. Those effects extend from subcellular levels such as genetic effects to effects on individuals (alterations of fitness or traits of individuals, such as changes in the morphology, behaviour, or demographic rates of natives (Lockwood et al. 2007)), populations or communities of species, up to effects on ecosystem processes (Parker et al. 1999). An example of a genetic effect is the hybridization of species, which may affect native species population growth (Lockwood et al., 2007). For example, In New Zealand, there is genetic evidence of interbreeding between the invasive Australian red back spider, *Latrodectus hasseltii*, and the endemic katipo spider, *L. katipo* (Vink et al., 2008). Therefore, *L. hasseltii* is a hazard for *L. katipo*, which also seems to be displaced both by *L. hasseltii* and another non-native spider (Vink et al., 2011). Other ecological mechanisms by which invaders change native species' populations include competition,

predation, and herbivory. Population effects can change community composition if the invader adversely impacts the dominant species structuring the ecosystem or more than one species. For example, also in New Zealand, species such as ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*), cats (*Felis catus*), ferrets (*Mustela furo*), and stoats (*M. erminea*), have contributed to the extinction of at least nine bird species in New Zealand, changing the native community composition (Dowding and Murphy, 2001). Changes in population sizes, individual behaviour, or community structure can alter flows of materials through ecosystems and natural disturbance regimes (Lockwood et al. 2007).

Much attention concerning biodiversity loss has focused on impacts of exotic vertebrates and plants (Brockerhoff *et al.* 2010), and non-native arthropods have received less attention (Saccaggi et al. 2016). Nevertheless, a few arthropods are among the most notorious invasive alien species due to their ecological impacts (Kenis et al., 2009; Brockerhoff et al., 2010). For example, the European elm bark beetle (*Soclytus multistritatus*) is the principal vector of Dutch elm disease (*Ceratocystis ulim*), which has devastated elm populations in north-eastern United States (Pearce et al., 1975; Aukema et al., 2010; Lee et al., 2011; Jacobi et al., 2013). Another noteworthy example, is the common wasp (*Vespula vulgaris*) in New Zealand, which adversely affects native birds and invertebrate biodiversity by harvesting honeydew of beech trees more efficiently and aggressively than the native fauna, in addition to preying on them (Toft and Rees, 1998; El-Sayet et al., 2009). Although key species with significant impacts are well documented, there is normally a little information on non-native species ecological impacts (Kenis et al., 2009; Saccaggi et al., 2016). However, any successful introduction of a new species into an ecosystem is likely to cause direct and indirect effects on native biodiversity (Blackburn et al., 2014). Although not all non-native species in a region are deeply studied, it is known that about 3,900 non-native arthropods are calculated to be established in continental North America (Langor et al., 2009), though this is likely a large underestimate (Langor et al., 2009) and over 2,000 are established in New Zealand (Brockerhoff et al., 2010).

1.2 Risk assessment of invasive organisms

Risk assessment to prevent the establishment of invasive organisms has been conducted for many decades. In 1951, the International Plant Protection Convention (IPPC) treaty was established to reduce the risk of plant pests and pathogens spreading around the world through trade of plants and plant products (IPPC 1997). The convention adopts international standards for phytosanitary measures (ISPMs) recognised by the World Trade Organization to provide guidance to all trading nations on measures to protect productive ecosystems around the world. Among the ISPMs are a number of guidelines for pest risk analysis and assessment whose structure has been used to assess the risk of a wide range of taxa establishing in new global regions. The most important part of a risk assessment process for an invasive species follows the invasion process continuum (see below). Pest risk

assessment is necessary to determine appropriate actions to interrupt or prevent 'the continuum of success' of the species because management efforts to mitigate the impact of any invasive species incurs significant economic, environmental and social costs (Gilbert et al., 2012). Clearly, the prevention of alien species introduction is the most cost-effective way forward (Hulme et al., 2009), because it is more economical than managing their potential consequences. According to ISPM11 (2013), the conclusions from pest risk assessments are used to decide whether risk management is required and the strength of measures to be used. Pest risk management is the process of identifying ways to react to a perceived risk, evaluating the efficacy of these actions, and identifying the most appropriate options. Finally, the IPPC and the principle of "transparency" requires that all trading countries and signatories to the Convention should, on request, make available the rationale for phytosanitary requirements (FAO, 2003).

Risk analysts often conceptualise the invasion process as occurring along a continuum from species arrival to the establishment and impact on the new ecosystem. It requires knowledge of species' characteristics relevant to invasion processes, which can be conceptualized as occurring along an introduction-naturalization-invasion continuum comprising introduction, survival, reproduction, dispersal and spread (Richardson et al., 2000; Blackburn et al., 2011). A species becomes invasive once it has completed the continuum, although not all species complete the different stages (Richardson and Pyšek, 2012). Some of the terms commonly used to describe a species introduced in a new area are 'non-native', 'exotic', 'alien', 'nonindigenous' and 'introduced'. Although, those terms are considered synonyms (Krueger and May, 1991; Masterson, 2007), some scientists have combined them to refer to specific phases of the continuum. For example, 'invasive alien species' (IAS) are frequently defined as the subset of alien species that have negative impacts (McGeoch et al., 2010), while 'alien' and 'non-native' species, are taxa that are introduced outside of their natural range either intentionally or unintentionally by a human agency, but do not necessarily have known negative impacts (IUCN, 2000; Masterson, 2007). I choose use the term non-native in most of this research because it allows a greater level of consistency.

To identify which non-native species are most likely to harm a recipient ecosystem, risk analysts investigate a species potential to traverse each stage of the invasion continuum by taking into account many different factors. The first stage of the invasion is arrival as a result of the transportation of individuals to new areas, and the assessment involves identification of the pathways and origin of those species. The second stage is establishment of those species, which is the process of forming a persistent population and depends on abiotic and biotic factors, such as climate suitability and habitat availability (Hulme 2009). The last stage is the spread, or expansion of the species to suitable habitats and interaction with the surrounding ecosystem (Vanhanen, 2008). If a species has high potential to

traverse the invasion continuum, and therefore reach this last stage, then it is likely to have effects on the new ecosystem.

Those three stages are assessed by the risk assessment process, which can be broadly divided into three interrelated steps, 1) pest categorization, 2) assessment of the probability of introduction and spread, and, 3) assessment of potential economic consequences including environmental impacts. The environmental impact assessment includes impact on threatened or valued species, biodiversity, ecosystems services or social impacts (Burgman et al., 2014).

1.3 Tools for risk and impact assessment

Two of the most common ways that arthropods are unintentionally introduced are as contaminants, typically associated with an imported commodity, or as stowaways or hitchhikers, normally associated with a transport vector (Hulme et al., 2008; McNeill et al., 2011; Saccaggi et al., 2016). However, not all the non-native arthropods associated with a commodity or a transport vector will be able to establish in the recipient ecosystems. Environmental factors such as climate suitability, host availability and abundance have been identified as key factors influencing the likelihood of establishment of non-native phytophagous arthropods (Bacon et al., 2014) and are often used to assess invasion success. Other approaches used to determine invasion success in more general invasion biology involves the identification of community attributes that affect the susceptibility or resistance to invasion, and the identification of species' traits to help predict the invasion success (García-Berthou et al., 2005). All these factors are not only likely to affect establishment success and spread but also the impact of non-native species.

In the early stages of the development of the discipline of invasion ecology, researchers searched for general principles that could be applied widely across taxonomic groups (Pyšek et al., 2008). This endeavour resulted in general principles, such as the enemy release hypothesis, the biotic resistance hypothesis and evolution of invasiveness (Williamson, 1996). However, since then many studies have demonstrated that generalizations across taxa about the external factors and species traits that determine invasion success are elusive, and factors associated with invasiveness are better determined within specific taxa and specific habitats (Statzner et al., 2008; Whitney and Gabler, 2008).

Pyšek et al., (2008) suggest that most case studies have focussed on non-native species with an imminent or realized economic impact with a strong research bias toward pests of agriculture, horticulture and forestry simply because there is likely to be more information about them. Gilbert et al., (2012) point out that different factors and traits may apply to invaders of natural ecosystem. But most often there is little information on the environmental impacts of arthropod invaders (Saccaggi et

al., 2016). Clearly, it would be helpful to identify determinants of invasion success and impact for arthropod invaders in natural ecosystems.

1.3.1 Non-native species inventories

A tool that has proven very useful for the determination of general patterns characterising invasive species and invaded habitats are the non-native species inventories (Kenis et al., 2007). Thus, the identification and listing of non-native species successfully established in different regions of the world is considered an essential tool for management of biological invasions (Ricciardi et al., 2000; Kolar and Lodge, 2001; McGeoch et al., 2010). Information about the non-native species already present in natural ecosystems is poor compared to modified ecosystems, but is essential for risk analysis. Those studies that have especially focussed on gathering information about non-native species in natural ecosystems, such as Phillips et al. (2008) and Martin and Paynter (2014), who created databases of non-native arthropods established in New Zealand, are particularly useful for the current intended research. Phillips et al. (2008) found a total of 181 cases of accidental (n=151) and intentional (n=30) introductions of non-indigenous invertebrates or pathogens, which have had negative impacts on semi-natural or natural ecosystems in New Zealand and overseas. Phillips et al. (2008) scored the impact in every case of non-native beetle and spider species on New Zealand and North American natural ecosystems. Martin and Paynter (2014) compiled a database of 624 pest-host records of non-native herbivorous invertebrates in New Zealand, 143 of which fed on indigenous plants. All these studies have suggested non-native species key characteristics influenced their establishment and impact success on natural ecosystems, but in this research, I intend to analyse these databases to help understand different patterns of invasiveness in different natural ecosystems. For example, it is frequently argued that continental communities are more resistant to invasion than island communities (Mooney and Cleland, 2001; Martínez et al., 2007; Corlett, 2010) due to their higher species diversity (Herben 2005), but also because of the larger trade volumes, which increases the potential pathways for non-native species to reach far off regions (Hulme, 2009; Pyšek et al., 2009). Higher species diversity on continental communities presents non-native species with more competition, predation and parasitism, and fewer unoccupied niches, making establishment and spread more difficult. In contrast, islands have lower species diversity, with biotas that are more specialized, less competitive and more frequently endemic (Herben 2005). Thus, islands have simplified food webs, unsaturated communities and more vacant niche space (D'Antonio and Dudley 1995). If an island habitat is disrupted or modified, non-native species might have adaptations that allow them to be more competitive and faster colonizers than native species (Gillespie et al., 2008; Malubres-Olarte et al., 2014). New Zealand has a native biota that exemplifies the lower species diversity observed on many isolated oceanic islands because entire functional groups, such as snakes, terrestrial mammals, colonial bees, wasps and ants are absent or greatly under-represented (Allen and

Lee 2006). Although island communities are expected to be more invasible than continental communities, supporting evidence is lacking. Thus, this thesis will investigate if natural ecosystems in New Zealand are more invisible than those in North America.

1.3.2 Determining the effect of abiotic and biotic factors in invasion success

Climatic suitability

Once non-native species present in a new environment have been identified and listed, factors influencing their establishment and invasion success can be also studied. It is thought that the key determinants of non-native species success in new ecosystems are likely to be primarily climate suitability and host availability.

Climate is a principal factor affecting the biology and evolution of poikilothermic species (Andrewartha and Birch 1945; Gutierrez and Ponti, 2013). Seasonal climate patterns are crucial for species survival during transport, but are also critical for successful development and persistence in a new area. Moreover, climatic extremes can impede reproduction (Andrewartha and Birch, 1945). Temperature, in particular, profoundly affects insect growth rates, fecundity, mortality and movement. Therefore, climate is a key factor limiting arthropod distributions (Bacon et al., 2014), and climatic similarity between native and invaded regions is considered a prerequisite for invasion success (Thuiller et al., 2004; Bellard et al., 2016).

Several modelling approaches exploit the influence of climate on species survival, reproduction and spread to help predict risks from invasive species. When the species of concern has been insufficiently studied, predictions based on correlations between the climate in the area of origin and the area of concern can be used. Such models are often referred to as climatic niche models (Jarvis and Baker 2001; Yonow et al. 2004). Other models are more straightforward and involve a simple climate match using some form of similarity measure for key temperature and moisture variables. Some examples of climate matching algorithms are the simple Regional Match Climates module in CLIMEX (Sutherst et al. 2007) and CLIMATCH (Crombie et al. 2008). Other modelling approaches involve phenological models based on species development rates in relation to temperature, which have been used for decades to help evaluate probabilities of pest establishment and spread (Javis and Baker 2001; Venette et al. 2010). Climate models often use a range of climatic variables to assess the suitability of a region for species establishment. A phenological model, however, uses only temperature available during the species development period to assess the likelihood of a pest becoming established in the new region (Jarvis and Baker, 2001). A common modelling approach includes what are referred to as correlative species distributions models (SDMs). SDMs establish statistical relationships between present-day geographical distributions and climate variables to project species future distributions (Evans et al.

2015). MaxEnt (Phillips et al. 2010) and other correlative species distribution models, for example those used by Senay et al. (2014), are used to project future changes in geographical ranges of species, but also, in conservation ecology to estimate extinction rates, examine the efficacy of existing reserve system and prioritize biodiversity conservation efforts (Porfirio et al. 2014). Finally, mechanistic species distribution models (also referred to as process-based models) such as CLIMEX (Sutherst et al. 2007) are another option. Mechanistic models differ from correlative models in that they consider how the environment constrains physiological performance at a given location (Evans et al. 2015). Thus, the future distribution of a species is predicted through a process of elimination, whereby regions that hinder physiological performance to the degree that the capacity for survival, growth or reproduction is compromised are excluded from the final distribution (Kearney and Porter, 2009).

Most studies using those modelling approaches assume that species' ecological requirements are conserved over space and time (niche conservatism), and species' geographical occurrence is mainly correlated with climate variables (Li et al., 2014). However, in its native range a particular species might be subject to dispersal limitations and specific biotic interactions that prevent it from colonizing all suitable conditions. As a consequence, when in a new range they might expand towards a climate not available in the native range, which may be considered a niche shift (Li et al. 2014). Although evolutionary changes of the invasive species that may cause a niche shift, are difficult to predict, as Wiens et al. (2010) reviews, several studies show that climatic niches of invasive populations may change significantly relative to the species native range. Often it is hard to judge just how precise predictions of species distribution are just based on climatic similarities (Sax et al. 2007). For those reasons, species distribution of climate matching models used to predict potential invasions may have a limited capacity, because of the assumption that species distributions are basically limited by climate (Duncan et al. 2009; Li et al. 2014).

Host presence and phylogenetic affinities

Host availability, on the other hand, is crucial for successful colonisation by phytophagous invertebrates (Niemelä and Mattson, 1996; Bacon et al., 2014). This factor may have a stronger influence on arthropod invasion success than climate (Bacon et al. 2014; Bebber 2015). In a review of the changing distributions of non-native pests and their causes, Bebber (2015) concluded that the potential to adapt to new climates and hosts is not taken into account by predictions based on climatic factors alone, and non-native pests can usually establish wherever their hosts occur. Given the importance of host presence and abundance on the establishment success of non-native herbivore species, this might be able to explain non-native species presence, as has been demonstrated by previous studies, such as that of Bebber et al. (2014), when analysing global patterns of crop pests and pathogen distributions. The presence and abundance of potential hosts and their taxonomic relationships with ancestral hosts are important factors for pest establishment in new regions (Niemelä

and Mattson, 1996). For example, Davies et al. (2005) and Fridley et al., (2007) demonstrated a positive relationship between plant species diversity and establishment of non-native plant pests and pathogens at large spatial scales. They explain this by suggesting that non-native plant pests and pathogens are more likely to find a suitable hosts in regions with higher plant diversity, as a factor that would increase the probability of finding a suitable host species. Plant host similarity between regions predisposes them to successful interchange herbivore species (Niemelä and Mattson 1996). For example, most invasive phytophagous insects in North American forests are European. Taxonomic affinities between the two continents, mean immigrant European species are likely to find potential congeneric and confamilial host plants in North America (Niemelä and Mattson, 1996). Thus, this thesis will investigate if floristic similarity between regions and floristic diversity usefully complement climate similarity to predict non-native phytophagous arthropod presences.

Gilbert et al. (2012) and Gilbert et al., (2015) have recently pointed out that taxonomic affinities between regions arise from historical and contemporary evolutionary links and showed that evaluating the evolutionary structure of the host ranges of plant pests is useful for pest risk analysis. Undoubtedly, closely related plant species are likely to be susceptible to the same pathogens and pests because morphological, chemical, and life-history traits are phylogenetically conserved (Gilbert and Webb 2007). Thus, plant phylogenetic distance between potential hosts can be used to give a rapid empirical estimate of the susceptibility of a large number of plant hosts to novel pests and pathogens, as shown by Gilbert et al. (2012) and Gilbert et al. (2015) in recent research.

However, many studies of invasive phytophagous insects and plant diseases only consider agricultural host plants (Bacon et al. 2014; Bebber et al. 2014) and have a low representation of natural ecosystems (Gilbert et al. 2012). One reason is that wild hosts are usually less abundant than agricultural hosts, particularly in Europe (Bacon et al. 2014). However, by not considering the plant diversity of the region of interest we might seriously underestimate the invasive potential of some non-native species. For example, the brown marmorated stink bug, *Halomorpha halys* (Hemiptera: Pentatomidae) is a highly polyphagous insect known to feed on more than 400 hosts (MacLellan, 2013); this includes economically important crops but also native plants (Bakken et al. 2015), and so for a comprehensive risk assessment of the pest all its known hosts need to be considered. Moreover, when introduced to a new range, the non-native species might be able to expand its host range onto secondary hosts and ultimately shift its host if it cannot find a preferred host (Agosta 2006; Lefort et al. 2014). However, some authors have argued that true host shifts are rare (Bacon et al. 2014), although there are records of pest species shifting host to species that are closely related to their native species (Bertheau et al. 2010). Thus, plant phylogenetic distance will be used in this study to predict relative impacts on individual New Zealand native plants.

1.3.3 Non-native species impact assessment

There is a critical need in general invasion ecology to quantify, evaluate, compare and predict the magnitudes of impact of different alien species (Blackburn et al. 2014; Nentwig et al. 2010). Quantifying impacts helps decision makers to prioritize their efforts to regulate and manage pests (Nentwig et al., 2010). Normally, management prioritizes species with obvious impacts. To prioritize some species against others, Nentwing et al. (2010) and Blackburn et al. (2014) suggest that we need to be able to rank the different species, and that can only be done by quantifying their impact within categories. There is an extensive literature on risk assessment methods for evaluating the risk of non-native or alien species establishments, and those methods normally include some kind of impact assessment (Kumschick and Richardson 2013). But there are also many impact assessment frameworks available in the literature that have been developed independently from any risk assessment (e.g. Parker et al 1999; Sandvik et al. 2013).

While there is an extensive literature on both risk assessment systems and impact assessment systems, there is little agreement on how impacts are incorporated in the risk assessment and how impacts should be compared among invading taxa and ecosystems (Parker et al. 1999; Essl et al. 2011; Kumschick and Ridchardson 2013). Therefore, comparing the effects of different invasive species on different levels of ecosystem organization for prioritization and management is a challenging task. That is why, in recent years there has been increased effort to create a standardized tool to quantify and compare impacts among taxonomic groups and geographic regions (Nentwig et al. 2016). A noteworthy example is the 'generic impact scoring system' (GISS), which was first developed by Nentwig et al. (2010) to evaluate the level of impact of alien mammals in Europe by using published evidence rather than expert opinion. Since then, the GISS has been modified to adapt to other taxonomic groups such as birds (Kumschick and Nentwig 2010), alien fish (van der Veer and Nentwig 2014), terrestrial invertebrates (Vaes-Petignat and Nentwig 2014), aquatic invertebrates (Laverty et al. 2015), and plants (Novoa et al. 2016), becoming one of the most used frameworks based upon the literature.

Although the original GISS relies just on published evidence, some of its adaptations combine published evidence with expert assessment. That is the case of two particular adaptations: the prioritization framework suggested by Kumschick et al. (2012) that includes impact scoring and stakeholder opinions, and the adaptation of the GISS to align with the new impact scheme of the Global Invasive Species Database (GISD). The latter was implemented by the Species Survival Commission (SSC) of the International Union for Conservation of Nature (IUCN) Red List categories and criteria that Blackburn et al. (2014) developed. Impact classifications that rely on expert assessments of uncertain information are commonly subject to bias and uncertainty (Kynn, 2008). For example, one set of

experts attributed more damage to invasive species in their own country than elsewhere, and regarded economic impacts as more severe than environmental impacts (Dahlstrom Davidson et al., 2013). In group assessment, Burgman (2005) emphasised the added bias introduced via dominant group members. Such uncertainties are a challenge for invasive species risk managers to incorporate in their decision-making process. Thus, an important question in this thesis is to evaluate whether the use of expert elicitation will help the improvement and incorporation of non-native species impact classifications in formal risk assessments.

1.4 Proposed research

The overall aim of this research is to improve the risk assessment of non-native arthropod species potential establishment and impact in natural ecosystems by attempting to answer the following research questions, 1) Are the impacts of non-native beetles and spiders in continental and oceanic island ecosystems different? 2) Does knowledge of flora similarity between the native and invasive range and plant diversity in the invasive range provide useful complementary information to climate suitability assessments to predict successful establishment of non-native invertebrate herbivores? 3) Can phylogenetic affinities of plants be a good predictor for phytosanitary risk of non-native invertebrate herbivores? 4) Are impact assessments by experts using published non-native species impact assessment frameworks better than random attributions of impact levels?

The specific objectives to answer these questions are:

Objective 1: Revise the taxon-specific database developed as part of the Phillips et al. (2008), by adding new records of established species of phytophagous beetle and spiders in New Zealand and North America, and reclassify their impacts to analyse and compare their impacts in the two geographic regions and identify the potential factors related to their differences (Chapter 2).

Objective 2: Determine whether floristic similarity between regions and floristic diversity, are useful complements to climatic similarity for risk assessment of the potential impact of non-indigenous insect invertebrates in native ecosystems (Chapter3).

Objective 3: Determine if phylogenetic affinity analysis of potential plant hosts between regions, gives useful predictions to evaluate the relative impacts on individual plants and ecological systems, using known existing invasive plant pests in New Zealand indigenous ecosystems (Chapter 4).

Objective 4: Review the different impact classification frameworks available in the literature and test if assessments using well-established ecological impact classifications that use statements about important consequences, as severity categories or values, are better than random attributions of impact levels. This will help to identify and understand the sources of uncertainty related to impact classification systems to help future development of robust classification schemes (Chapter 5).

Chapter 2

Impacts of non-native beetles and spiders in natural ecosystems of continents and oceanic islands

2.1 Introduction

Biological invasions have accelerated along with increases in global trade of commodities, and international travel. It is estimated that each nation now has thousands of non-native species (Pimentel 2011), some of which were intentional introductions, such as crop and livestock species, but most were accidental (Liebhold et al. 2016). Collectively, non-native species cause changes in both managed and natural ecosystems (Pimentel 2011; Blackburn et al. 2014), and are considered one of the biggest threat to biodiversity together with habitat destruction (Glowka et al. 1994). Their ecological impacts can occur at different levels of biological organization and at different spatial scales (Kenis et al. 2009). Evaluating, comparing and predicting impacts of non-native species is necessary to develop and prioritise mitigation measures (Blackburn et al. 2014), and a greater ability is needed to predict which species present the highest risk.

Novel environments present several filters that non-native species must traverse to succeed as invaders. Human colonization, global trade and travel have helped many species to overcome biogeographic barriers (Wilson et al. 2009). Once past the biogeographic filter, abiotic similarities between the invaded and recipient environment are needed for species establishment. Such filtering may explain why non-native species from particular biogeographic origins are over-represented in some invaded ranges; successful invaders reflect the trade history of the recipient region and its habitat similarities with regions of origin (Niemelä and Mattson, 1996). Thus, invaders may not be a random selection of species (Karatayev et al. 2009).

Communities of non-native pests in a geographic region may be dominated by species from particular geographic origins (Niemelä and Mattson, 1996; Langor et al. 2009). For example, non-native arthropods on woody plants in Canada are predominantly European (Langor et al. 2009). Over-representation of particular biogeographic origins may be linked with historical trade patterns, and climatic and biogeographic similarities between the source regions and invaded regions. Biogeographic relationships can be important due to co-evolutionary arms races between herbivores and their host plants. As host defences evolve, herbivores, parasites and parasitoids must also evolve the means to overcome those defences. Therefore, many herbivores become specialised to only feed on a phylogenetically narrow range of hosts (Bernays and Graham 1988). While generalist predators may

be less constrained by host phylogeny (Memmott et al., 2000; Pekár et al. , 2012), phylogenetic relationships are also likely to be important for specialised predators and parasitoids which are strictly associated with particular host insects (Brockerhoff et al. 2010). Arthropod generalist predators, for example, are known to feed on a wide host range and different trophic levels (Snyder and Evans, 2006). Therefore, while I expect that non-native phytophagous insect invasions will be restricted by host phylogenetic relatedness, non-native arthropod generalist predators will not be.

When invading a new range, the availability of suitable hosts will be a determinant of non-native herbivores and parasites successful establishment (Niemelä and Mattson, 1996). Phylogenetic constraints on host species may be particularly important for phytophagous insects because they are often host-specific (Ødegaard et al. 2005). Niemelä and Mattson (1996) reviewed invasive phytophagous insects in North America and noted that most insects were rather host-specific because they fed on the same tree genera in North America as in their native European range. Geographic and fossil evidence has shown that North America was geographically connected to Europe and Asia during the late Cretaceous and the Tertiary periods, which explains why 48% of North American native vascular plant genera are also native to Eurasia (Qian 1999). Similarly, Ridley et al. (2000) suggested that herbivorous insects that originate from other Gondwanan remnants may represent the greatest risk to New Zealand's native plants. New Zealand separated from Gondwana approximately 80 million years ago (Cooper and Millener, 1993), much of its fauna and flora may have arrived by dispersal in the last 23 million years after a period of submergence in the Oligocene (Goldberg et al. 2008).

Other characteristics of recipient environments also influence invasion success. It is frequently argued that continental communities are more resistant to invasion than island communities (Mooney and Cleland 2001; Martínez et al. 2007; Corlett 2010), mainly due to differences in species diversity (Herben 2005). Both theory and empirical data suggest that continents do have greater species diversity, which will present non-native species with more competition and fewer unoccupied niches to make establishment and spread more difficult. In contrast, islands have lower species diversity, and island species are more often highly specialized, endemic and less competitive (Herben 2005). Thus, islands have simplified food webs, unsaturated communities and more vacant niche space (D'Antonio & Dudley 1995). If an island habitat is disrupted or modified, non-native species are more likely to colonize it because they tend to be more competitive (Gillespie et al. 2008).

New Zealand has a native biota that exemplifies the lower species diversity observed on many isolated oceanic islands. Entire functional groups, such as indigenous snakes, predatory terrestrial mammals, colonial bees, wasps and ants are under-represented in New Zealand's biota (Allen and Lee 2006). I expect that island communities, such as those in New Zealand, will generally be more invasible than

continental communities, because they are generally less diverse with lower competition and more vacant niches.

Much attention concerning biodiversity loss has focused on the impacts of non-native vertebrates and plants (Allen and Lee, 2006; Brockerhoff et al. 2010). However, non-native insects should also be considered due to their sometimes large direct and indirect effects on native biodiversity (Kenis et al. 2009). An estimated 3,900 non-native species of arthropods are established in continental North America (Langor et al. 2009), and over 2,000 in New Zealand (Brockerhoff et al. 2010).

I have built on previous work (Phillips et al. 2008) and available expertise to evaluate and compare in a semi-quantitative review the impacts of non-native spiders and several groups of non-native beetles on native biota in North America and New Zealand. Globally, beetles and spiders are species-rich, comparatively well known, include numerous successful invaders, and differ markedly in characteristics such as trophic level and degree of host/prey specialisation. Beetle adults and larvae are often host specific, because plant-insect associations are strongly influenced by plant chemical, morphological, and life-history traits (Herms and Mattson, 1992; Coley and Barone 1996; Brockerhoff and Bain 2000; Lewinson et al. 2005). Host-specificity is often determined by adult behaviour, especially host selection and oviposition, while the host-feeding larvae sometimes have a broader host range, perhaps restricted by limited mobility (Jaenike 1990). In contrast, spiders are often generalist predators (Eichenberger et al. 2009; Líznarová et al. 2013). They tend to capture and consume a wide variety of invertebrate prey, especially if they are web-builders (Pekár et al. 2011).

With potential differences between continental and island ecosystems, and the influence of host-specificity and host phylogenetic affinities, I postulated and tested the following hypotheses for non-native beetles and spiders in North America and New Zealand:

1) Non-native beetles that feed on North American or New Zealand native plants have different geographic origins. Non-native beetles in North America originate primarily from locations with host plants that are phylogenetically closely related to those in North America, such as Eurasia. In contrast, non-native beetles that feed on New Zealand native plants are more likely to originate from other Gondwanan fragments such as Australia and South America.

2) Spiders tend to be generalist predators and therefore should be less constrained by prey phylogeny. Thus, I expect non-native spiders in North America and New Zealand to originate from a wider range of locations.

3) Island ecological communities, such as New Zealand's, will generally be more invasible than continental ecosystems, because island communities are less diverse with lower competition and more

vacant niches. Thus, I expect both non-native spiders and beetles to have greater impacts in New Zealand than in North America.

To test my predictions, I compiled a database of non-native spiders and several groups of non-native beetles known to be established either in New Zealand or North America from published lists and reports. I then classified each species according to its geographic origin and impact on native biota of North America and New Zealand, and compared impacts between taxa, geographic origins and invaded ranges.

2.2 Methods

2.2.1 Study taxa

The non-indigenous taxa chosen for study were a group of predators and a group of herbivores, spiders (Araneae) and beetles (Coleoptera) in particular. Of the beetles, weevils (Curculionidae) were included in this study because they are a relatively well documented group with some species of high-impact. Longhorn beetles (Cerambycidae) and true bark beetles (Curculionidea: Scolytinae) were also added to that selection because they are amongst the most high-impact wood and bark borers invaders. However, ambrosia beetles (Curculionoidea: Scolytinae) were excluded because they do not feed directly on wood, but on wood-inhabiting ectosymbiotic fungi introduced into the gallery made by the beetle (Beaver 1989). In this paper, longhorn beetles, true bark beetles and weevils are henceforth collectively referred to as 'beetles'.

As herbivores, beetles have frequently been transported in association with plant material and plant-based products (e.g. Brockerhoff et al. 2006, Liebhold et al. 2012). They impose biotic stress on plants that can influence plant growth and vigour (Bezemer et al. 2008), and can also have numerous other effects on plant communities and ecosystems, such as altering carbon and nutrient flows, displacing native species, vectoring plant and insect diseases, increasing apparent competition, and hybridizing with closely related native species (Coyle et al. 2008; Kenis et al. 2009; Brockerhoff *et al.* 2010). For example, species of beetles that have recently established in North America are currently having, or are expected to have, considerable impact on indigenous ecosystems, production forests, and/or urban trees (Pinski 2005; Haack 2006).

Large number of spider species have been unintentionally introduced through human colonization and trade. Once in a new geographic range, these predators can have extensive impacts at multiple trophic levels (Hogg and Daane 2014). They may suppress prey populations more than native predators, making prey species more vulnerable to stochastic extinction forces, and drive biodiversity losses at regional scales (Salo et al. 2007). Mechanisms by which alien spiders harm native spider species include

web invasion and usurpation, intra-guild predation, prey and web site competition, and hybridization (Bednarski et al. 2010; Brockerhoff et al. 2010; Hogg and Daane 2011; Jakob et al. 2011; Houser et al. 2014). A New Zealand example is the Australian redback spider, *Lactrodectus hasseltii* (Theridiidae), that feeds on New Zealand native scarab beetles, including *Prodontria modesta*, *P. lewisii*and *Mimopeus* sp. which are range restricted and nationally endangered (Vink et al. 2011; Bryan et al. 2015). The Australian redback spider also displaces the New Zealand endemic *Latrodectus katipo*, and there is genetic evidence of hybridization in the wild (Vink et al. 2011).

2.2.2 Data collection: List of invasive invertebrates

The ISI Web of Science and Google Scholar were used to search for information regarding the presence and impact of invasive beetle and spider species in North America and New Zealand. Search terms included the taxonomic group of interest, their invasiveness (synonyms of invasive), and the invaded geographic range.

Key words used for invasiveness were "non-native", "invasive", "alien", "established", "nonindigenous", "introduced", and "exotic". To specify the taxonomic group, key words were "weevils", "Curculionidae", "beetles", "Cerambycidae", "long-horn", "true bark", "Scolytinae", "spiders", and "Araneae". To specify geographic range, key words were "North America", "United States", "Canada", and "New Zealand". The logical operator "AND" was used to combine different key words. Additionally, a search on each species was made to gather information about its impact on natural ecosystems, taxonomic classification, invasion range, native range, and degree of specialization. Key words used for this second search were the scientific name of the species, its synonyms, and its common name in its native and invaded ranges. In some cases, domain experts were consulted to provide additional information and help estimate species impacts.

2.2.3 Classification criteria

The classification criteria used to define species impacts were created by Phillips *et al.* (2008), and evaluated "the effect of the invader on the abundance of one or more native species, or on the functioning of an organism or an ecological process". The classifications comprised four categories (none, minor, occasionally major and major) and are described in Table 2.1.

Table 2.1 Impact criteria used to classify non-native species to categories of impact on natural ecosystems.

Impact categories			
None (none)	**Minor (minor)**	**Occasionally major (omajor)**	**Major (major)**
No impact on native species or natural ecosystems. Closely related to human activities and urban areas. No information confirming its presence in natural ecosystem.	Recorded feeding on native species and/ or present in natural ecosystems. Low population density and/ or small geographic range, but a moderate impact per capita. No direct effect on live organisms.	Significant impact on native species, but restricted in time or space. No significant impact (moderate), but widespread distribution.	From moderate to wide geographic range high local density, and clear significant impact.
Specific examples			
Non-native beetles feeding on introduced plant species, such as *Anilaus amplicollis* in New Zealand and *Hypera meles* in North America.	Non-native dead-wood borers, which may compete with native species and alter decomposition processes, such as *Macrorhyncolus littoralis* in New Zealand.	Non-native spiders displacing native species in synanthropic environments, such as *Linyphia triangularis* in North America.	Non-native wood borers killing native hosts, such as *Tetropium fuscum* in Canada (North America).

I used Fisher's Exact Test, which is employed when sample sizes are small and there are cells on the contingency table with values below 5, to test relationships both between impact and invaded range, and between impact and biogeographic origin. To classify the origin of the different species studied, biogeographic regions were used (Afrotropical, Australasian, Cosmopolitan, Holarctic, Indomalayan, Nearctic, Neotropical, Palearctic, and Pantropical). Analyses were conducted using R version 3.3.0 and the R package *stats* (R Core Team 2013). Graphics were created using the R package *ggplot2* (Wickham, 2009).

2.3 Results

2.3.1 Non-native species in North America

According to published lists and reports (O'Brien & Wibmer 1982; Arnett *et al.* 2002; Aukema *et al.* 2010), 208 non-native beetle species are established in North America (195 Curculionidae, from which 15 are from the Scolytinae subfamily, and 13 Cerambycidae), of which 180 (86.5%) were accidentally introduced and 28 (13.5%) were intentionally introduced for weed biological control, which were not included in the further analysis (Table 2.2). From the accidentally introduced species, 80 species (44.4%) were recorded as having some impact on North American native plant species. Fifty six (31.1%) have had minor impacts, 17 (9.4%) have had occasionally major impacts (*omajor*), and seven (3.9%) have had major impacts (Figure 2.1). The species names and their impact classifications are presented in Appendix 1.

I recorded 111 non-native spider species (Figure 2.1 and Table 2.2) as established in North America (Petrunkevitch 1911; Guarisco 1999; Berrian, Ruiz and Clark 2010; Paquin *et al.* 2010a; Calixto *et al.* 2013; Ovtcharenko, Tanasevitch and Zakharov 2014; Vink unpublished data). Sixty six (59.4%) have had no impact because they are not known to occur in natural ecosystems or impact on native species (Houser, Ginsberg & Jakob 2014). Forty one species (36.9%) do occur in natural ecosystems and have had minor impacts. Five species (4.5%) have had occasionally major impacts (*omajor*) on native species in synanthropic ecosystems.

2.3.2 Non-native species in New Zealand

According to published literature (O'Brien & Wibmer 1982; Arnett *et al.* 2002; Phillips *et al.* 2008), 67 non-native beetle species are established in New Zealand (58 Curculionidae, from which five are from the Scolytinae family, and nine Cerambycidae) (Figure 2.1 and Table 2.2), of which four (6%) were intentionally introduced for weed biological control. From the accidentally introduced species, 11 (17.7%) have been recorded in native ecosystems (Kuschel 1990; Brockerhoff and Bain 2000; Phillips et al. 2008; Phillips and Vink in preparation), and so are classified as having minor impacts. Most of these records were reviewed by Kuschel (1990), who presented a case study of the records compiled by the Forest Health database, maintained by Forest Research, Rotorua (E. Brokerhoff personal communication, September 2016). Host plant records were collected from fragments of native forest on the north side of the Manukau Harbour, Auckland City. Four species of beetles have been formally recorded feeding on New Zealand native flora. Four others that feed on driftwood were also included in this category because they could have indirect effects on native ecosystems via competition (Phillips et al. 2008), and by changing chemical, physical, and/or structural biotope characteristics (Blackburn et al. 2014).

Sixty nine non-native spider species are established in New Zealand (Vink et al. 2004; Forster and Forster 2005; Phillips et al. 2008; Paquin et al 2010b; Vink unpublished data) (Figure 2.1 and Table 2.2). Twenty five (36.2%) have had no impact on natural ecosystems, and 41 species (59.4%) have had minor impacts, mainly because they have been recorded in New Zealand natural ecosystems (Berndt 1998; Ward et al. 1999; Alley et al. 2001; Derraik et al. 2001). Three (4.3%) have had major impacts (see Appendix A.1).

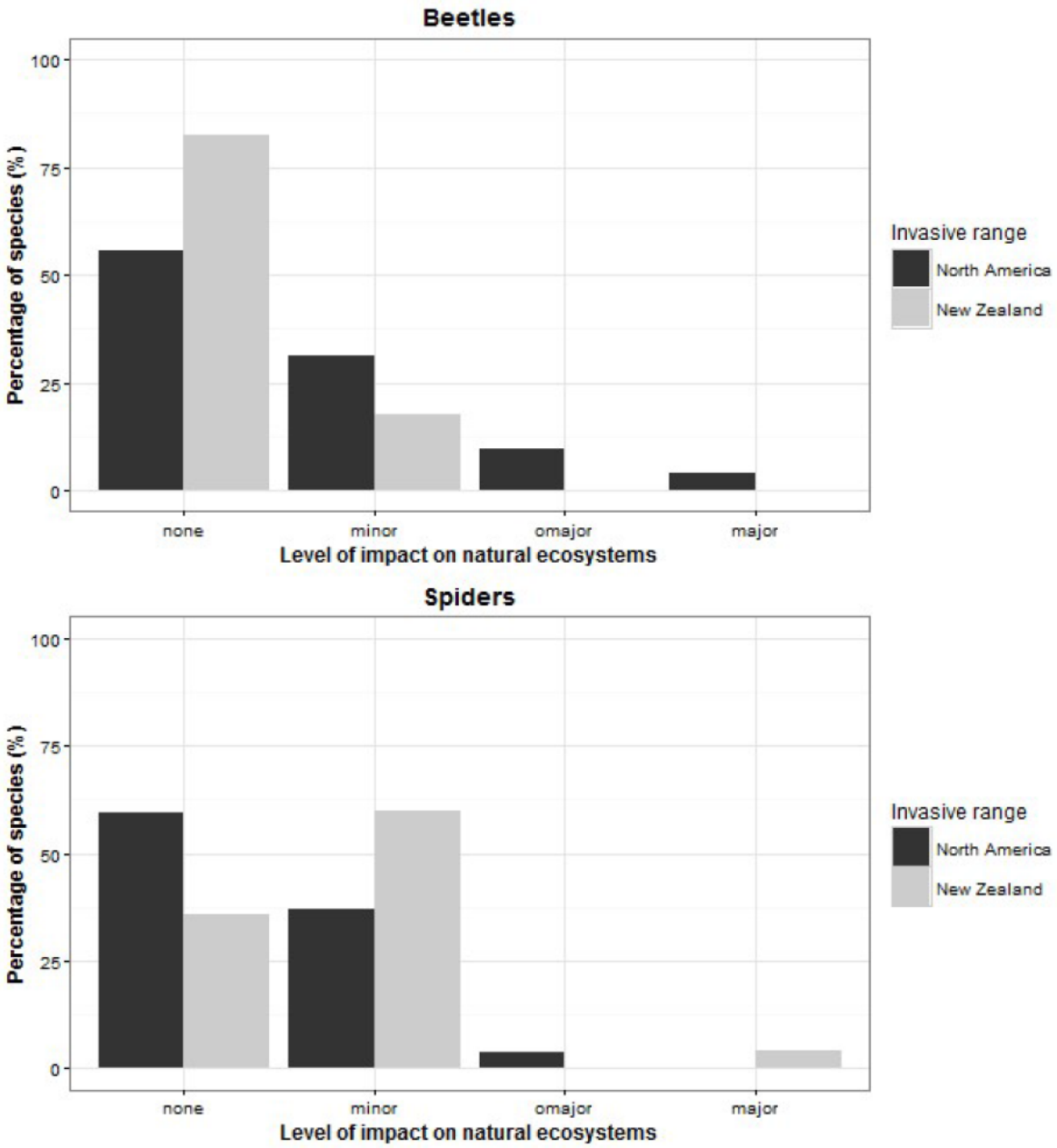


Figure 2.1 Percentage of non-native beetle and spider species that have invaded North America and New Zealand and their impact on natural ecosystems and native species in their invaded range.

2.3.3 Impact analysis of alien beetles and spiders in their invaded range

According to the results from the Fisher's exact test (Table 2.2), impacts of accidentally introduced spiders and beetles within the same target region are significantly different for North America and New Zealand (p-value = 0.03152 between taxa in North America< p-value < 0.001 between taxa in New Zealand), although in New Zealand differences in the level of impact between spiders and beetles are greater. Moreover, when comparing the level of impact of each taxa for the two target regions, the analysis showed that the differences were also significant (p-value < 0.001 for beetles and p-value < 0.001 when comparing levels of impacts of the non-native species between North America and New Zealand).

Table 2.2. Contingency table with the number and proportion of species per level of impact (biological control agents not included). Also, the Fisher's exact test results for the taxa and invaded range considered separately.

Region	Taxon	Impact				Fisher's exact test p-value	
		None	Minor	Omajor	Major	**Within region**	**Within taxon**
North America	Beetles	**100**/180 = 0.56	**56**/180 = 0.31	**17**/180 = 0.09	**7**/180 = 0.04	North America	Beetles
	Spiders	**66**/111 = 0.59	**41**/111 = 0.37	**4**/111 = 0.04	**0**/111 = 0.00	0.0315	< 0.001
New Zealand	Beetles	**51**/62 = 0.82	**11**/62 = 0.18	**0**/62 = 0.00	**0**/62 = 0.00	New Zealand	Spiders
	Spiders	**25**/70 = 0.36	**42**/70 = 0.60	**0**/70 = 0.00	**3**/70 = 0.04	< 0.001	< 0.001

For the analyses of taxon differences I tested for significant impact difference between North America and New Zealand (second column of Fisher's exact test p-value, where shading indicates the content of each contingency table) , and for the invaded range analysis I tested for significant impact differences between beetles and spiders within each region (first column of Fisher's exact test p-value).

2.3.4 Geographic origins and impact of North American alien species

In North America, 61 (76.2%) of the 80 non-native beetles that have had impacts on native ecosystems were Palearctic, and nine (11.2%) were Neotropical (Table 2.3). Species from both geographic regions had a range of impacts from minor to major. The remaining 10 species were Indomalayan, Australasian, Cosmopolitan, Nearctic or from unknown origins, and they had minor or occasionally major impacts. For spiders, 45 non-native species have had impacts, of which 27 (60%) are Palearctic and nine (20 %) are cosmopolitan. Spiders from both these groups have had minor or occasionally major impacts. The remaining nine species were Neotropical, Australasian, Holarctic or of unknown origin.

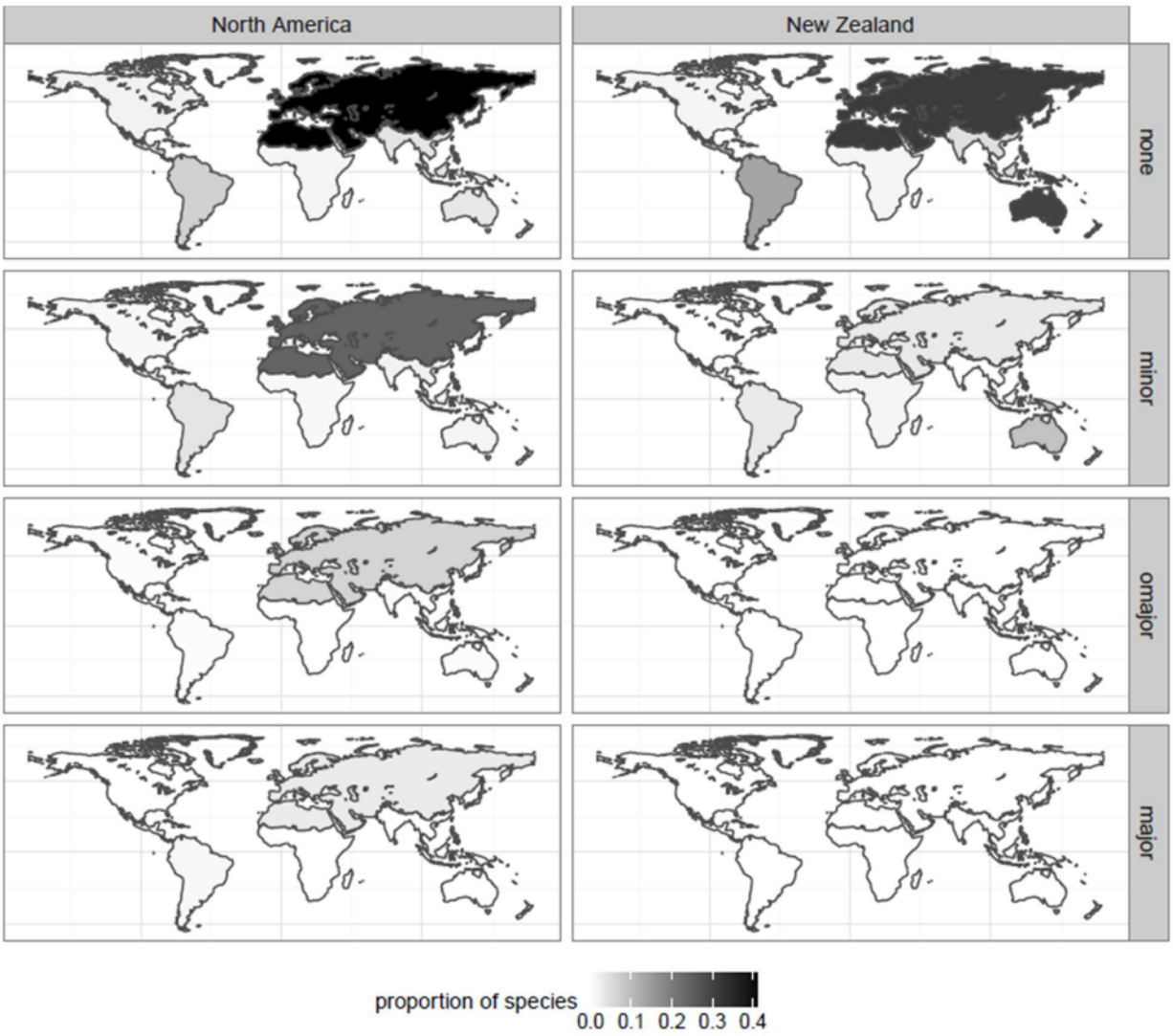


Figure 2.2 Origins and impacts of non-native beetles in North America and New Zealand (X axis, the target region) and the level of impact (Y axis). Proportion of species goes from zero (white) to 0.42 (black). Note that in North America, which belongs to the Nearctic ecoregion, I found some non-native species that originated in the same ecoregion but out of North America (e.g. North part of Mexico). Similarly, many non-native species in New Zealand come from the same ecoregion, Australasia, but have been accidentally introduced from other regions of the same ecoregion (e.g. Australasia).

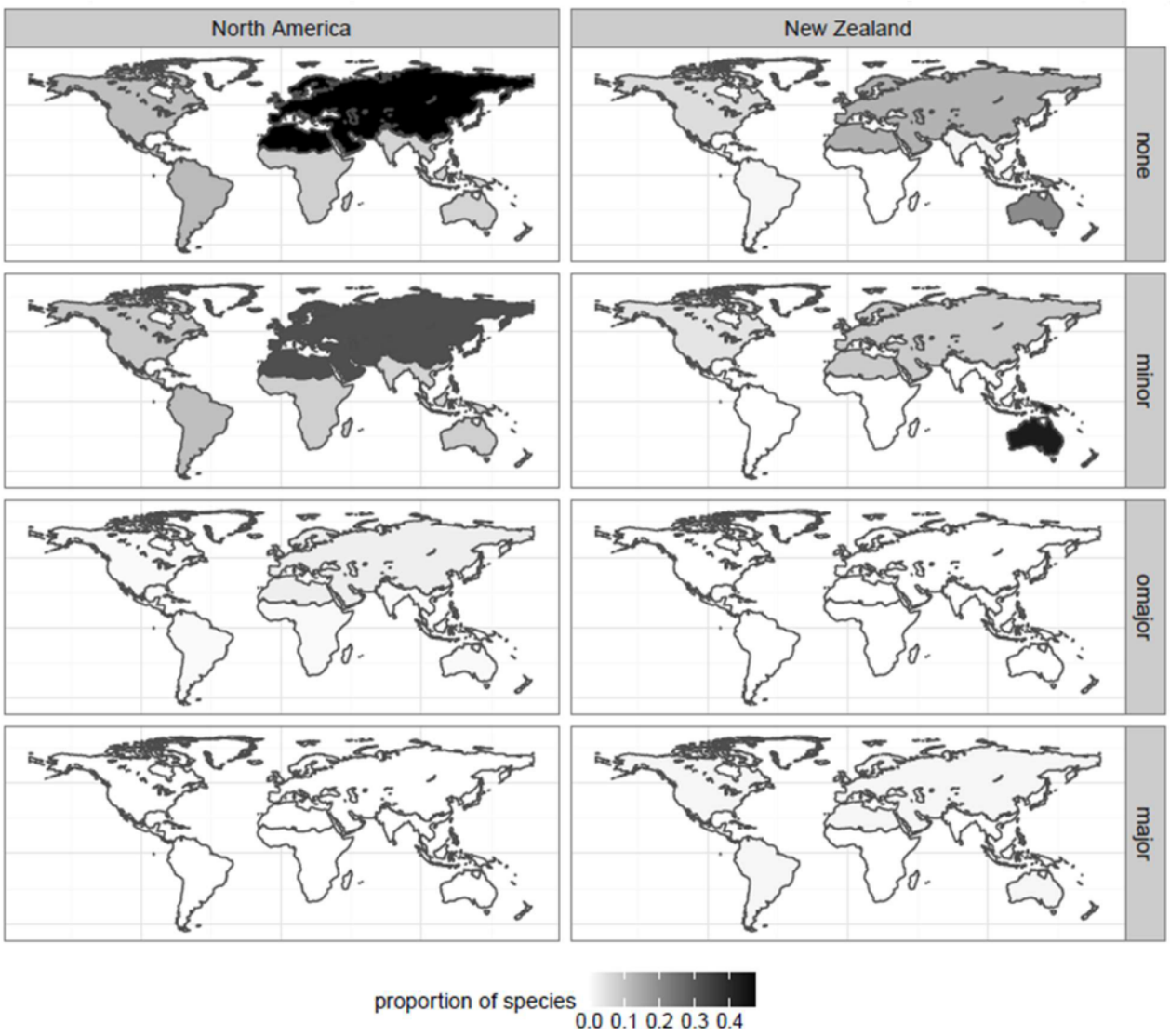


Figure 2.3 Origins and impacts of non-native spiders in North America and New Zealand (X axis, the target region) and the level of impact (Y axis). Proportion of species goes from zero (white) to 0.47 (black). Note that in North America, which belongs to the Nearctic ecoregion, I found some non-native species that originated in the same ecoregion but out of North America (e.g. North part of Mexico). Similarly, many non-native species in New Zealand come from the same ecoregion, Australasia, but have been accidentally introduced from other regions of the same ecoregion (e.g. Australasia).

2.3.5 Geographic origins and impact of New Zealand alien species

In New Zealand, six (54.4%) of the 11 species of introduced beetles that have had minor impacts on native species are Australasian, three (27.3%) are Neotropical, two (18.2%) are Palearctic, and one (9.1%) is Afrotropical (Figure 2.2 and Appendix A.2). Of the 43 introduced spider species that have had impacts, 42 (74.4%) are Australasian, and the remaining 11 species are either Holarctic, Nearctic, Palearctic, Pantropical, Neotropical or of unknown origin (Figure 3 and Appendix A.2). The three species that have had major impacts in New Zealand are Australasian, African and Holarctic.

2.3.6 Geographic origin statistical analysis

There was no significant association between biogeographic origin and impact for non-native beetles in North America (p-value = 0.9561) and New Zealand (p-value = 0.4661). Similarly, there was no significant association between biogeographic origin and impact for non-native spiders in North America (p-value = 0.7219). However, there was a significant association for non-native spiders in New Zealand (p-value = 0.03).

2.4 Discussion

My first hypothesis was that non-native beetles in North America will originate from locations with host plants that are phylogenetically closely related to those in North America, such as Eurasia. In contrast, non-native beetles that feed on New Zealand native plants should originate from other Gondwanan fragments such as Australia and South America. The results showed the majority of the species having impact on North American native ecosystems found in this study are Palearctic (78% of the species studied). The predominance of Palearctic species may be explained both by historical trade between North America and the Old World, but also by similarities in the vegetation and climate in these regions (Aukema et al. 2010). Several authors found that the majority of European phytophagous insects in North America have colonized the same tree genera that they feed on their native range, and that they are rather diet specialized (mono- or oligophagous) (Wheeler and Henry 1992; Mattson et al. 1994). But if their host plant is not available, because of their host-specificity, non-native species establishment in the new environments will depend on the abundance and availability of taxonomically closely related ancestral hosts (Niemelä and Mattson, 1996; Ødegaard et al. 2005) or the presence of their host plants as introduced non-native plant species. It was expected that phylogenetic relatedness between host species in the native and invaded regions would also explain the non-native beetle impact in their invaded range. However, in this study, no significant relationship between the geographic origin, and therefore the assumed phylogenetic relatedness of their hosts in both regions, of the non-native beetles in North America and their impacts was found.

The relationship between the geographic origins, and therefore the assumed phylogenetic relatedness of their host, of the non-native beetles in New Zealand and their impact was also not significant.

Contrary to what I expected, some Palaearctic non-native beetles were recorded feeding on New Zealand native plants. All of them are generalist species (polyphagous). Similarly, in their study of exotic invertebrates in New Zealand's indigenous ecosystems, which included some non-native Curculionidae but also other phytophagous insect families, Brockerhoff et al. (2010) emphasised that most northern hemisphere non-native insects in New Zealand feed on introduced northern hemisphere plants. Also, coinciding with what I found, Brockerhoff et al. (2010) pointed out that several relatively polyphagous non-native invertebrates have been recorded feeding on native plants, such as *Epiphyas postvittana* (Lep.:Tortricidae) and *Canatreus aspersus* (Gastropoda: Helicidae). In particular, native flora probably provides temporary or accidental hosts because of the widespread distribution of some non-native beetles' exotic host plants (Phillips et al. 2008).

Despite the predominance of non-native beetles from geographic origins historically connected to New Zealand (Australasian, Neotropical and Afrotropical), we found that their impacts on New Zealand indigenous ecosystems are rare and minimal. New Zealand shares many plant families with Australia, New Caledonia and South America, as these regions were all part of the Gondwana supercontinent that broke up 85 M years ago (Wardle 2002). Clearly, their relative proximity increased the potential for dispersal between them (Puente-Lelièvre et al. 2013). However, host phylogenetic relationships might not be as important as I expected for phytophagous insects in New Zealand, especially if the island resource allocation (IRA) hypothesis is true. The IRA hypothesis states that isolated oceanic islands have simple food webs which include fewer natural enemies of plant-feeding insects, such as predators and parasitoids (Kay 2006). Therefore, plants evolved to rely more on their own defences against herbivory by phytophagous invertebrates (Kay 2006). As a result they have greater physical and chemical defences to reduce the probability of being attacked (Le Guigo et al. 2012). However, this might not be true for other non-native phytophagous invertebrate species. Martin and Paynter (2014) reviewed and analysed literature recording adventive Acari and Insecta herbivores in New Zealand attacking indigenous plants. The authors demonstrated that adventive herbivores feeding on New Zealand indigenous plants varied significantly according to arthropod order and family and their degree of polyphagy. In their study, they gathered and analysed information of 624 adventive herbivore species and found that Hemiptera was the most numerous order of non-native arthropods feeding on New Zealand indigenous plants. Moreover, in a study that compared trends of non-native Hymenoptera between New Zealand and Europe, Ward and Edney-Browne (2015) stated that biogeographic origin was an important filter for non-native species. When comparing intentional with unintentional non-native Hymenoptera present in New Zealand, Ward and Edney-Browne (2015) found that patterns on the biogeographic origin of the species in both groups were significantly different, and that Australasia significantly provided the greatest part of unintentional alien Hymenoptera. Therefore, the apparent agreement between my results and the IRA hypothesis

statements is probably due to the ecological characteristics of the specific taxonomic groups that I have studied.

The second hypothesis was that non-native spiders in North America and New Zealand will originate from a wider range of locations than beetles. My results showed there is a significant relationship between the geographic origin of non-native spiders and their impact in New Zealand, but that relationship is not significant for non-native spiders in North America. As Reed and Newland (2002) pointed out on a pest risk assessment of spiders associated with grapes, Australian spiders have a long history of establishment in New Zealand. The geographic proximity between Australia and New Zealand is likely to favour natural dispersal by ballooning between regions, but also the human assisted dispersal. Similar to my results, Kobelt and Nentwig (2008) found a high underestimation of alien spider species from the eastern Palearctic in Europe, which was attributed to the proximity between regions. Kobelt and Nentwig (2008) stated that the shorter the transportation distance, and therefore the exposition to extreme temperature and humidity conditions, the higher is the survival rate of hitchhikers. Moreover, long distance trade fumigation of containers is a common method to kill possible hitchhikers, which also reduces the number of survivors being transported but does not eliminate all of them (Reed and Newland, 2001; Koblet and Nentwig 2008). Additionally, some spider species are known to survive and recover well from prolonged periods of food deprivation (Froster and Kavale, 1989; Reed and Newland, 2002). *Latrodectus hasseltii* in particular, can survive long periods of starvation in cargo, and it seems that natural long distance dispersal is rare (Froster and Kavale, 1989; Vink et al. 2011).

The third hypothesis was that non-native spiders and beetles will have greater impacts in New Zealand than in North America. My results showed that North American natural ecosystems are more vulnerable to phytophagous insect invasion than those of New Zealand. In particular, 41% (86 species) of the alien beetle species that have established in the United States have some impact in natural ecosystems, but my results for non-native beetles do not support the hypothesis that continental ecosystems should be more resistant to invasive species than island communities. Some authors have hypothesized that North American forests could be especially sensitive to invasive arthropods partially due to their vast area and diverse ecosystems, which would increase the probability of finding a suitable host species ("environmental heterogeneity hypothesis") (Davies et al. 2005; Coyle et al. 2008; Liebhold et al. 2013). For example, MacDonald et al. (1989) found a positive relationship between native and exotic diversity in South Africa nature reserves. However, a negative relationship between native biodiversity and invasions of exotic species has also been found, confirming what is known as the "Associational resistance hypothesis" (Barbosa et al. 2009). For example, Cardinale et al. (2012) found that resistance to plant invasion generally increases with species richness in plant communities.

Those contradictory negative and positive relationships between native biodiversity and invasions of exotic species, is what is known as the "invasion paradox" and its resolution depends on the spatial scale of the study (Fridley et al. 2007). For example, Davies et al. (2005) were able to detect both relationships within the same data set with a change in scale. Therefore, over large spatial scales, such as this study, positive relations between the native biodiversity and biological invasions are found, because effects of site-wide extrinsic factors, such as resource availability and propagule supply rate, covary with the diversity to provide favourable conditions for exotics and natives (Levine and D'Antonio, 1999; Davies et al. 2005).

New Zealand natural ecosystems, on the other hand, are more vulnerable to invertebrate generalist predators than North American according to my results. Thus, island communities appear to be generally more invisible by generalist predators than continental ecosystems. North American natural ecosystems seem to be more resistant to non-native spiders than beetles, possibly because they have complex food webs and there are few empty niches. This would explain why, the most non-native spiders that have impacts in North America are synanthropic (Houser et al. 2014). It has been found that well-established native predator and/or pathogen populations might reduce the probabilities of competition with non-native species (D'Antonio and Dudley 1995), but they may also reduce the potential vulnerability of the non-native species to a top predator (Romanuk et al. 2009). Houser et al. (2014) in a study of competition between introduced and native spiders found that invasive spiders are more likely to negatively affect native spiders in simpler less productive landscapes, such as human-modified ecosystems. This could explain why I found that non-native invasive spider species in North America where having impacts on native species in disturbed or modified habitats (synantrhopic ecosystems). However, non-native spiders represent a potential threat because once non-native spiders are established and abundant in human modified ecosystems, such as agroecosystems, they can spread to adjacent natural habitats (Evans et al. 2011; Hogg and Daane 2014). In New Zealand, invasive spiders had relatively greater impacts on native species. Many New Zealand native invertebrates are highly endemic, especially spiders (Allen and Lee, 2006). Endemicity may have affected New Zealand native spiders' dispersal abilities making them less competitive, and could explain why some exotic spiders are dominant in disrupted natural ecosystems (Vink et al. 2008; Malumbres-Olate et al. 2013; Malumbres-Olate et al. 2014). However, some authors have argued that the global spread of some New Zealand native species suggests that they can also be strong competitor (Allen and Lee, 2006), although that may not be true for spiders, which seem to be at a particular disadvantage against Australian spider invaders. The low diversity of top predators in New Zealand food webs that could compete with or predate the non-native invasive species seem to be an advantage for invasive spiders, as theoretically based on the empirical data of food webs suggests (D'Antonio and Dudley 1995; Romanuk et al. 2009; Galiana et al. 2014). Spider invaders in New Zealand

also seem to have been able to find vacant niches, where they feed on naïve invertebrate species that are especially endangered or range restricted (e.g. *Lactrodectus hasseltii*) (Vink et al. 2011).

In summary, an ecological characteristic that seems to be an advantage for non-native invertebrates in New Zealand is their degree of polyphagy or host generality. Thus, the island community studied, New Zealand, is generally more invasible by host-generalist invertebrates than the continental ecosystem that was compared to, North America. With respect to phylogenetic relatedness, half of the non-native phytophagous beetles and spiders causing impacts in New Zealand native ecosystems were Australasian, and a quarter were Neotropical, with a native range in either South or Central America (Figure 3). While in North America, most of the non-native species studied are Palearctic, although the non-native beetle host-specificity was much more variable (Figure 4). Despite the absence of a significant relationship between impact and species-origin in my study, except for non-native spiders in New Zealand, the indication is that host phylogeny might play an important role in the impact of non-native invertebrate species in natural ecosystems. Future work could involve the study of the relative effect of the level of host-specificity of the taxon, and the phylogenetic affinities between the hosts in the native and invaded range on the invasion success of terrestrial invertebrate non-native species. That can then help policy makers and risk managers to prioritize their actions and efforts against species that can represent a serious threat for native ecosystems.

Chapter 3

Can measures of floristic composition improve predictions of non-native pest establishment success based on climate matching alone?

3.1 Introduction

Non-native arthropods pose a major threat to native biodiversity and economic activity worldwide (Brockerhoff et al. 2010; Pimentel et al. 2011). For non-native arthropods to successfully invade a new region, they need to overcome a continuum of abiotic and biotic challenges (Blackburn et al. 2011). Some important determinants of non-native pest species establishment are propagule pressure and environmental factors, such as climatic suitability and host availability (Williamson 1996; Leung et al. 2012). Once non-native pests have been introduced, they are only likely to survive in a new region if they encounter abiotic conditions similar to those in their native range (Walther et al., 2009), and if suitable hosts are available (Niemelä and Matson, 1996). Even though just a small fraction of potential non-native species successfully overcome all abiotic and biotic challenges and become established in a new range (Williamson 1996), the number of non-native species establishing in new regions keeps increasing, often with enormous impact (Aukema et al. 2010; Bradshaw et al. 2016). An estimated 3,900 non-native arthropod species are established in continental North America (Langor et al. 2009), and over 2,000 in New Zealand (Brockerhoff et al. 2010).

Climatic similarity between the native and invaded region of a species is considered a prerequisite for invasion success (Thuiller et al. 2004; Bellard et al. 2015). Many studies show that climatic suitability is a key factor limiting the distribution of arthropods (Bacon et al. 2014), due to climate's impact on many life history traits and fitness (Shelton 1973; Loetti et al. 2011). For insects, temperature profoundly affects growth rates, fecundity, mortality and movement (Ciota et al. 2014). Therefore, many studies have used climatic and phenological models to predict establishment and spread of non-native insect pests (Jarvis and Baker 2001; Venette et al. 2010). Some phenological models, that use empirical data can help assess pest risk by relating the likelihood of an insect species becoming established in a new region with the temperature available during its developmental period (Jarvis and Baker 2001). However, when the species of concern has been insufficently studied, predictions based on correlations between the climate in the area of origin and the area of concern can be used. Such models are often referred to as climate matching or climatic niche models (Jarvis and Baker 2001; Yonow et al. 2004). Climatic niche models can also be used to estimate future threat areas assessing the biosecurity risk over wider a geographic perspective (Kriticos 2012). The simpler Regional Match

Climates module in CLIMEX (Surtherst and Maywald 1985) can also be used to make rapid initial assessments of species' establishment risk (C. Phillips and J. Berry, personal communication); it estimates temperature and rainfall similarities between a single site or region and locations elsewhere in the world (Surtherst et al. 2007). While matching species' environmental (primarily climatic) requirements has been widely used to predict potential species distributions, some authors have argued that it is unclear how precise predictions based on a species current distribution can be (Sax et al. 2007). In a review of the changing distributions of non-native pests and their causes, Bebber (2015) concluded that due to the non-native species adaptive evolution ability to exploit novel climatic conditions and their increased migration via human activities, they could potentially establish wherever their hosts are available. Thus, for some species, such as those with high adaptive evolution ability, climate matching alone might underestimate their potential distribution. Therefore, host availability is also crucial for successful colonisations of phytophagous invertebrates (Niemelä and Mattson, 1996; Bacon et al., 2014).

In their study of the invasion of North American forests by European phytophagous insects, Niemelä and Mattson (1996) showed that, at a continental scale, non-native pest establishment in new environments depends on the presence of hosts and the hosts' taxonomic relationships with the pests' natural hosts. Other research, addressing hypotheses about relationships between plant species diversity and non-native phytophagous species invasions, have found the relationship to be positive in some studies and negative in others (Guyot et al. 2015). Davies et al. (2005) and Fridley et al. (2007) pointed out that the relationship depended on the spatial scale of the research. These latter studies observed positive relationships at large spatial scales and negative relationships at smaller scales. At smaller scales the presence of non-host plants can interfere with non-native species' establishment on host plants, reducing the rate of development and spread of pests and pathogens (Fridley et al. 2007; Guyot et al. 2015). By contrast, at a continental scale Niemelä and Mattson, (1996) showed that floristic similarity between regions predisposed them to successful interchanges of herbivores. For example, the majority of phytophagous insects that have successfully invaded North American forests because of human colonitzation are European due to plant taxonomic affinities between the two continents. These affinities mean that European species invading North America are more likely to find host plants amongst species from the same genera or families as their native hosts (Wheeler and Henry 1992; Mattson et al. 1994; Niemelä and Mattson 1996). Such floristic affinities between regions arise from regions' historical and contemporary links. The importance of different links would be difficult to tease apart, but regional floristic similarities can be measured (see Methods).

Bebber (2015) suggested that the invasion success of quarantine arthropods worldwide largely follows host range. However, studies that just consider agricultural host plants when investigating relationships between host plant distributions and arthropod invasions will overlook the effect of non-crop host plants (Bacon et al. 2014; Bebber et al. 2014). Crop pests and pathogens can also infest

congeneric and confamilial non-crop species, as has been recorded in New Zealand (Goldson et al. 2015). Therefore, omitting non-crop hosts can misrepresent a pest's true host range and inaccurately predict invasion risks. Nevertheless, pest risk assessments are often strongly influenced by economic priorities and practical limitations, and host plant records for many pests are biased towards crop plants (Pyšek et al. 2008; Gilbert et al. 2012).

My study spans New Zealand (north and south islands), Kansas (USA, inner-continental) and Virginia (USA, coastal continental) and asks how well climatic similarity, floristic similarity and floristic diversity explain relationships between these regions' non-native beetle faunas only. I expect that non-native species distribution predictions that include floristic similarity will be more accurate than those that use climate predictions alone; this not least because plant distributions are also influenced by climate (Bebber et al. 2014; Bacon et al. 2014; Bebber, 2015), but also because of the assumption that plant assemblages or associations indicate realised or potential host availability. Because there is more potential host availability associated with diversity, I also expect non-native beetle diversity to be positively correlated with floristic diversity. For that reason, I compare the influence of climate and plant community similarity, as well as plant diversity, on non-native beetle occurrences. I analyse the diversities and similarities of plant assemblages at the chosen locations for crop and non-crop plants, both separately and together.

3.2 Methods

I tested the influences of climate, floristic similarity and floristic diversity on the presence of non-native beetle species in three regions; New Zealand, Kansas and Virginia. These regions were selected because of beetle species data availability. Floristic diversity and floristic similarity were determined using the Germplasm Resources Information Network (GRIN) taxonomy for plants (USDA 2015). The presence of established populations of the invasive non-native beetle species listed in Chapter 2 for New Zealand, Kansas and Virginia comprised the dependent variable. To evaluate the influence of the variables of interest, at least five non-native beetle species occurrence points around the world were needed, and each of the non-native beetle species included needed to be present in at least two of the target regions (Table 3.1). Climatic similarity was estimated using the regional match climates function of CLIMEX (Surtherst et al. 2007), floristic similarity was estimated using the Jaccard similarity index, and plant diversity was estimated using Faith's phylogenetic diversity. For each target region, the measures of climatic similarity and floristic similarity and diversity were compared with other regions where the beetles are present.

Table 3.1 Species of non-native beetle species in each target region.

Species	Kansas	Virginia	New Zealand
Scolytus multistriatus	X	X	X
Scolytus schevyrewi	X	X	
Scolytus rugulosus	X		
Otiorhynchus ovatus	X	X	
Anthonomus grandis	X	X	
Hypera postica	X	X	
Otiorhynchus sulcatus	X	X	X
Rhinocyllus conicus	X	X	X
Sitona cylindricollis	X	X	
Sitona hispidula	X	X	
Sitophilus zeamais	X	X	
Listoderes costriostris		X	X
Listronotus bonariensis			X
Phoracantha semipunctata			X
Otiorhynchus rugosostriatus		X	X
Gonipterus scutellatus			X
Pantonomus cervinus		X	X

3.2.1 Study scale

Climatic and floristic similarities were estimated between New Zealand, Kansas and Virginia and 379 other world regions. These regions comprised whole countries except USA, Australia and Brazil, which were divided into states, and Canada, which was divided into provinces. Such divisions reduced variation in land area between regions.

The 64 regions that contained none of the beetle species shown in Table 1 were excluded from the analysis. To help prevent the 'double-zero problem', countries, states and territories where all non-native beetle species in this study, were absent according to GBIF and Crop Protection Compendium (CABI), were excluded from the database.

I also excluded 82 regions that had fewer than 20 plant genera recorded in the GRIN database (http://www.ars-grin.gov/~sbmljw/johnindex.html accessed June 2015, USDA 2015; further details given in 'Plant Similarity' section), based on an assumption that this indicated under-sampling. The remaining regions analysed totalled 233.

3.2.2 Climate matching

To match the climates of New Zealand, Kansas and Virginia with other world regions, I used the regional match climates algorithm of CLIMEX Version 3 (Sutherst et al. 2007). This algorithm analyses matches between a set of 'home' locations and a set of 'away' locations. My home locations were New Zealand, Kansas and Virginia, and my away locations were the other regions defined in the previous section. The regional match climates algorithm uses temperature and rainfall data to calculate Composite Match Indices (CMIs) between one away location and every home location. It then assigns the highest CMI to the away location, and repeats this process for every away location (Sutherst et al. 2007). The climate dataset used was "WorldGrid30.mm", which is supplied with the CLIMEX software.

3.2.3 Floristic similarity

The GRIN database for plants (accessed June 2015, USDA 2015) was used to define the presence of native and non-native plant genera in each region. Similarities between all regions were quantified using the Jaccard similarity index (Jaccard 1912), which circumvents the 'double-zero problem' when shared absences may not indicate ecological similarity of regions (Legendre and Legendre, 1998). The Jaccard similarity index was calculated using the statistical software R version 3.3.0 (R Core Team 2013) with the package *vegan* (Oksanen et al. 2015).

Three sets of Jaccard indices were calculated to estimate similarities between each of the three target regions and the other world regions: one for all plant genera present (J), another for the native flora present (NJ), and a third for the non-native or exotic plant genera present (EJ). Thus, high values on floristic similarity between regions indicate the presence of congeneric plants.

3.2.4 Floristic diversity

The GRIN taxonomy (USDA 2015) was used to create a list of all known plant genera and their presence in each world region. Phylocom (Webb et al. 2008), which is a tool that supports studies of the taxonomic structure of communities, was used to calculate phylogenetic metrics for each region. The R20120829 phylogenetic tree for plants, derived from the Angiosperm Phylogeny Group III reconstruction, was used to calculate phylogenetic distances between plant genera (Bremer et al. 2009) (Chapter 4). The floristic diversity of each region was estimated using Faith's phylogenetic diversity (Faith 1992; Kembel et al 2010), as a measure of phylogenetic α-diversity, and is the sum of all the branch lengths that separate taxa in a community (Faith 1992; Kembel et al. 2010). Faith's phylogenetic diversity (PD) for each region was calculated using R version 3.3.0 (R Core Team 2013) with the package *Picante* (Kembel et al. 2010). Faith's phylogenetic diversity for native (PDN) and exotic (PDE) genera for each country, state or province was also calculated.

3.2.5 Statistical analysis

To assess the effects of climatic and floristic similarity, and plant diversity on the presence of beetle species in New Zealand, Kansas and Virginia, five sets of generalized linear mixed models (GLMMs) were created. These models included: 1) climatic similarity alone ('climate' model, independent variables: CMI), 2) floristic similarity and diversity ('all plants' model, independent variables: J, PD), 3) native and exotic floristic similarity and diversity as separate variables ('native/exotic' model, independent variables: NJ, EJ, PDN, PDE), 4) floristic and climatic similarity ('all plants & climate' model, independent variables: J, PD, CMI), and 5) native and exotic plants combined with climate similarity ('native/exotic & climate' model, independent variables: NJ, EJ, PDN, PDE, CMI). For each model, the binomial family, logit link and beetle species name as a random effect were used. To assess differences in the effects of climate similarity, floristic similarity and plant diversity between target regions and non-native beetle species, generalized linear models (GLMs) for three beetle species were created. These beetles were those that occurred in all three target regions (Table 3.1). The individual species models (GLMs) allowed a more detailed study of the influence of the variables on species presence than GLMMs results.

Because related non-native pest species are expected to respond similarly to new biotic and abiotic conditions due to phylogenetic inheritance (Manchester and Bullock 2000), phylogenetic auto-correlation was also considered in my models. Different forms of taxonomic hierarchy, such as subfamilies nested within families and genera nested within subfamilies, were tested as random effects to account for potential non independence (Blackburn and Duncan 2001; Nentwig et al. 2010). No significant differences were found between models using these additional random effects and those without them. Therefore, 'species name' was the only random effect included in my GLMMs.
For the GLMM calculation, *lme4* package was used in R (R Core Team 2013; Bates et al. 2014; Barton 2015). *MuMIn* was also used to calculate the conditional and marginal R^2 for the final model. Conditional R^2 accounts for of the variance explained by the random and fixed effects of the model and marginal R^2 is associated with the fixed effects (Nakagawa and Schielzeth 2013). For the individual species models, *stats* R default package was used for the GLM and ANOVA calculation, and *pscl* package for the calculation of the McFadden's pseudo r-squared, which can be interpreted as R^2 (McFadden 1979; R Core Team 2013; Jackman 2015). Moreover, the 95% confidence interval for each final model was calculated. If the 95% confidence interval of an independent variable did not include zero, it was considered significant (Gilbert et al. 2012).

For every set of models of GLMs and GLMMs, with the exception of the climatic similarity model which just has an independent variable, the linear dependence and correlation between the independent variables was assessed with the Pearson's correlation matrix and the variance inflation factors (VIF)

(Mansfield and Helms, 1982; R is my friend, 2013). For all the models except the climatic similarity model, several models were fitted that combined two-way interaction terms between pairs of variables. Model performance was tested using the correction of the Akaike's information criterion (AICc) (Akaike, 1973) and the *AICcmodavg* package (Mazerolle 2016) to select the best fitted model. AICc is AIC that corrects for finite sample sizes. AIC allows comparison between multiple competing models to choose the best approximating model according to its goodness of fit (Bolker et al., 2008; Symonds and Moussalli, 2011). Significant differences between models, according to the AICc, were tested using ANOVA. See supplementary material and Table 6 with the selected models according to the information criterion.

3.3 Results

3.3.1 General models (GLMM)

For predicting non-native beetle species presence, models that included both climatic and floristic similarity between target and other regions had better goodness of fit than models that included each variable separately (Table 3.2). However, models that included floristic variables alone had better fit than models that just included climatic similarity. For all target regions, the 'native/exotic & climate' models had the best fit.

Table 3.2 Conditional (R^2c) and marginal (R^2m) for each GLMM model for three target regions.

Model name		Kansas	Virginia	New Zealand
'climate'	R^2m	0.2557	0.2214	0.1991
	R^2c	0.3167	0.2817	0.3348
'native/exotic'	R^2m	0.3076	0.2936	0.5194
	R^2c	0.3764	0.3590	0.6279
'all plants'	R^2m	0.2568	0.2471	0.3233
	R^2c	0.3239	0.3117	0.4614
'native/exotic & climate'	R^2m	0.3491	0.3636	0.8066
	R^2c	0.4161	0.4272	0.8496
'all plants & climate'	R^2m	0.3270	0.3556	0.3602
	R^2c	0.3915	0.4164	0.4926

According to the 95% confidence intervals, which are significant if they do not include zero (Gilbert et al. 2012), CMI is significant for all target regions (in 'climate', 'native/exotic & climate' and 'Climate & All plants' models) (Table 3.3). Moreover, in 'all plants & climate' models, Jaccard similarity of all plants at genus level (J) is significant. However, in the 'native/exotic & climate' models, just the Jaccard similarity index of non-native plant genera (EJ) was significant for all target regions; the NJ Jaccard similarity index of native plant genera (NJ) was not significant for Virginia (Table 3.3).

Table 3.3 Results of each of GLMM models for the three target regions considering climate similarity and floristic variables.

Model name	Target region	Variables	Confidence interval	
			2.5%	97.5%
'all plants & climate'	**Kansas**	CMI	0.3704	0.6827
		GJ	0.6975	1.0340
		PD	-0.0493	0.3108
		CMI:GJ	-0.3885	-0.1252
		CMI:PD	0.0366	0.4336
		GJ:PD	-0.4288	0.0898
		CMI:GJ:PD	0.0319	0.4786
	New Zealand	CMI	0.2762	0.7026
		GJ	0.9808	1.4708
		PD	0.3580	0.7409
		CMI:GJ	-0.5752	-0.1987
		CMI:PD	-0.5318	-0.1030
		GJ:PD	0.3936	0.9566
		CMI:GJ:PD	-0.4776	0.0286
	Virginia	CMI	0.2043	0.4799
		GJ	1.0346	1.3927
		PD	0.1670	0.4698
		CMI:GJ	-0.8009	-0.5419
		CMI:PD	-0.0489	0.2769
		GJ:PD	0.0506	0.5904
		CMI:GJ:PD	-0.0351	0.3918
'native/exotic & climate'	**Kansas**	CMI	0.4160	0.7311
		EJ	1.3142	2.0049
		NJ	-1.0352	-0.4944
		PDE	0.6617	1.0699
		PDN	0.3441	0.7234
		CMI:PDN	-0.2662	0.0194
		EJ:NJ	-0.2217	0.0537
		EJ:PDE	0.1808	1.0885
		EJ:PDN	-0.4011	0.5691
		NJ:PDE	-0.0647	0.6638
		NJ:PDN	0.0363	0.8311
		PDE:PDN	-0.1785	0.0202
	New Zealand	CMI	0.3400	0.7649
		EJ	1.4444	2.4785
		NJ	-2.1966	-1.0452
		PDE	-1.2775	-0.1599
		PDN	-0.0031	0.4009
		CMI:EJ	-1.8009	-0.7741
		CMI:NJ	-0.7764	0.8573
		CMI:PDE	0.4158	1.5781
		CMI:PDN	-0.6771	-0.1342
		EJ:NJ	0.0449	1.1517
		EJ:PDN	-0.3029	0.0342
	Virginia	CMI	0.3368	0.6095
		EJ	0.5061	1.2609
		NJ	-0.0272	0.7194
		PDE	-0.0147	0.3408
		PDN	0.2729	0.5391
		CMI:EJ	-0.1609	0.6893
		CMI:NJ	-1.3886	-0.5317
		CMI:PDE	-0.0899	0.3224
		EJ:PDE	-0.1448	0.3889
		NJ:PDN	0.2746	0.6819

CMI = Composite Match Index; NJ = Jaccard similarity index of native plants at genus level; EJ = Jaccard similarity index of exotic plants at genus level; PDN = Phylogenetic diversity of native plants at genus level; PDE = Phylogenetic diversity of exotic plants at genus level; GJ = Jaccard similarity of all plants at genus level; PD= Phylogenetic diversity of all plants at genus level.

Plant diversity results were more variable between regions. For example the phylogenetic diversity of plant genera (PD) was significant in all regions except Kansas for the 'all plants & climate' models. In the 'native/exotic & climate' models, phylogenetic diversity of exotic plant genera (PDE) was significant

in all the regions except Virginia, and phylogenetic diversity of native plant genera (PDN) was not significant for New Zealand (Table 3.3).

3.3.2 Individual species models (GLM)

Similar to the results of the GLMMs, the GLMs for *Scolytus multistriatus*, *Otiorhynchus sulcatus*, and *Rhinocyllus conicus* that included climatic and floristic similarity had better goodness of fit than models that included these factors separately (Table 3.4). However, all the New Zealand models had much lower R^2 values than Kansas and Virginia models. Moreover, New Zealand 'climate' was the model with the lowest R^2 for the three species, particularly *S. multistriatus* (Table 3.4).

Table 3.4 R^2 for each of GLM models for the three individual species in the selected regions.

Species	Model name		Kansas	Virginia	New Zealand
Scolytus multistriatus	'climate'	R^2	0.3694	0.3763	$2.6054e^{-03}$
	'native/exotic'	R^2	0.4015	0.3986	0.2065
	'all plants'	R^2	0.4732	0.5028	0.1606
	'native/exotic & climate'	R^2	0.5266	0.5333	0.2128
	'all plants & climate'	R^2	0.5658	0.5849	0.1696
Otiorhynchus sulcatus	'climate'	R^2	0.1354	0.2627	0.0260
	'native/exotic'	R^2	0.3983	0.3236	0.0811
	all plants'	R^2	0.1493	0.1738	0.0597
	'native/exotic & climate'	R^2	0.4209	0.4072	0.0984
	'all plants & climate'	R^2	0.2157	0.3369	0.0645
Rhinocyllus conicus	climate'	R^2	0.3265	0.2343	0.0260
	'native/exotic'	R^2	0.2760	0.2354	0.0977
	all plants'	R^2	0.3450	0.3125	0.1119
	'native/exotic & climate'	R^2	0.4336	0.2986	0.1236
	'all plants & climate'	R^2	0.3535	0.3404	0.1439

In addition to the particular results for New Zealand given by the R^2 values, the importance of the independent variables in the models for the other two target regions, also differ. For the models that include both floristic and climatic similarity ('all plants & climate' and 'native/exotic & climate'), CMI is rarely significant, according to the confidence interval, and explains a low proportion of the deviance, except for *R. conicus* 'native/exotic & climate model (see Appendix B.2). While for Kansas and Virginia, CMI is always significant and explains most of the deviance (between 37.63% and 13.54%). For New Zealand models, PD and PDN, depending on the model, appear to be the more important variables according to the confidence interval and the deviance explained (between 16.09% and 3.99% for PD, and between 17.53% and 3.22% for PDN) for the three non-native beetle species.

3.4 Discussion

General models (GLMMs) and the individual species models (GLMs) supported the hypothesis that floristic similarity between regions in combination with plant diversity within a region better predicts the presence of non-native beetle species than models with climate similarity alone. However, including floristic and climate variables in the same model better predicted non-native beetle presence than models that included either variable separately.

Similar results were found by Bebber et al. (2014) when analysing global patterns of crop pests and pathogen distributions. Bebber et al (2014) found that crop pest and pathogen assemblages were strongly correlated with host distributions. Bebber et al. (2014) also found, from their analysis using models fitted by permutational multivariate ANOVA of crop pest and pathogen assemblages among countries, that climate also had a significant but small influence. Therefore, it has been suggested that modelling the distribution of the hosts through climatic variables may be a better approach than estimating the potential distribution of the pests alone (Bebber et al. 2014; Sutherst, 2014). Likewise, Bacon et al. (2014), when attempting to determine the factors needed to explain quarantine arthropod invasions in Europe, found that the probability of invasion increased mainly with host availability, but also with climate suitability. This was also the conclusion of Sax et al. (2007), who reviewed the ecological and evolutionary insights from species invasions for predicting species distributions after introduction or following climate change. Nevertheless, it must be acknowledged that introduced species and recipient communities evolve (Phillips et al. 2008), which can alter invasiveness and confound predictions (Whitney and Gabler 2008).

Most studies that investigate non-native species distributions or attempt to predict establishments, assume that species ecological requirements are conserved over space and time (niche conservatism), and that species' geographical occurrences are especially correlated with climate variables (Li et al. 2014). However, in the native range the species might be subject to dispersal limitations and specific biotic interactions and may be unable to colonize all suitable abiotic conditions. As a consequence, when in a new range they might expand into abiotic environments that were unavailable in the native range but become available in the invaded range (Li et al. 2014). Climate-matching approaches to predict potential invasions may be limited, because they assume species distributions are limited mainly by climate (Duncan et al. 2009; Li et al. 2014). However, studies such as that by Duncan et al. (2009), who analysed data on the introduction of five South African dung beetle species in Australia, have found that factors other than climate, such as dispersal limitation, resource limitation and the impact of natural enemies are major factors limiting the distributions of some species.

In addition, the importance of measures of climatic similarity for explaining non-native species distributions in this study seem to depend on the target region studied. In this study, climatic similarity between New Zealand and other regions of the world, where the non-native pests studied here are present, was much lower than for the other target regions studied. Moreover, individual species models for the three species present in all target regions showed even greater differences. This might have been due to the range and variability of New Zealand's climates, which vary from warm subtropical to cool temperate (NIWA, 2016). While such climatic variation can provide high levels of climatic similarity to many different regions of the world, such high climatic variability, partly explained by the high topographic diversity of New Zealand (Linder et al. 2014), might make non-native pest establishment predictions in New Zealand inaccurate. Nevertheless, the results show climatic similarity is an important variable that explains non-native beetle presence in New Zealand and elsewhere.

Host availability, which in this study was estimated by floristic similarity, seems to be a better indicator of non-native beetle distributions than climate. As Bebber (2015) concluded in his review of the changing distributions of non-native pests and their causes, the increased dispersal of invasive species is associated with human activities that help them establish wherever their hosts are found. Other studies have also highlighted the importance of accounting for host availability as well as climate. Although some authors have argued that true host shifts are very rare and unpredictable (Bacon et al. 2014), there are records of pest species shifting to hosts that are closely related to their native species. For example, Paine et al. (2011) in their review of native and exotic pests of *Eucalyptus* worldwide, highlight that some native lepidopteran fauna in Brazil that naturally feed on myracetous plants have switched to Eucalyptus. Therefore, even if the non-native pest can potentially expand its host range or ultimately shift its host, taxonomic affinities between hosts in their native and exotic ranges are expected to increase the probability of successful establishment (Niemelä and Mattson, 1996). In this study, taxonomic affinities were represented by the Jaccard similarity index, which was a measure of floristic similarity at genus level between regions.

Non-native beetle presence was significantly correlated with plant diversity in two regions, but not Kansas. Moreover, when native and exotic plant diversity were considered separately in this study, native plant diversity was not significant for non-native beetles in New Zealand, whereas it was significantly and negatively related to exotic plant diversity. However, non-native pest presences in both US states were significant and positively related to exotic and native plant diversity, except for exotic plants in Virginia. Although my results are variable and inconclusive, not only for the general models but also on the individual species models, if a larger number of non-native pest species were included in the analyses, outputs for the general models might be more consistent with previous studies. Thus, at large spatial scales, such as this study, positive relations between plant diversity and

non-native pest presence will be found as suggested by Davies et al. (2005) and Fridley et al. (2007) after extensive reviews of the literature. A particular and recent example is given by Liebhold et al. (2013) who analysed the geographical distribution of US non-native forest pest species; they demonstrated that the rate of establishment of invasive insect pests in the US was positively correlated with tree species diversity because it increased the pest's probability of finding a suitable host.

In conclusion, my study indicates to that include floristic similarity measures between countries within climate similarity analyses, geographic risk assessments of non-native organisms is likely to improve. For that reason, my recommendation is to use climate matching as part of a rapid assessment for a species, then combine measures of climatic and floristic similarity to identify areas at risk. Such an approach is likely to help resource allocation for risk assessments and the subsequent identification of potential pest organisms through more biologically based models. Despite the evident advantages of including floristic similarity within the geographic risk assessment, my data only allowed the analysis of floristic similarity at a coarse resolution with one measure of floristic similarity per region. On the other hand, the Match Climates function in CLIMEX allows the identification of the threat of pest establishment at a finer resolution, at a grid of 30 degrees cells in this case (Sutherst and Maywald, 1985; Sutherst et al. 2007; Kriticos, 2012). Future research should focus on gathering quality data to analyse the influence of regional plant and climate similarity on non-native pest species presence, to identify particular threat regions globally.

Chapter 4

Using phylogenetic signal analysis to predict the potential host range of non-native invertebrate herbivores and to identify species likely to invade natural ecosystems

4.1 Introduction

Herbivore-plant interactions are of great interest to ecologists. For example, herbivore richness and its variation among host-plant species was first studied by Southwood (1961) and has been widely studied ever since. In terrestrial ecosystems, it was demonstrated recently that plant species richness is a significant predictor of herbivore richness (Basset et al. 2012). Reviews by Lewinsohn et al. (2005) and Lind et al. (2015) revealed how a growing number of studies are now considering the importance of evolutionary relationships and the phylogeny of host plants when analysing insect-herbivore community structure and composition. Supporting such studies has been the recent development of a range of phylogenetic tools that allow ecologists to detect the influence of evolutionary history on contemporary ecological patterns and interactions (Webb et al. 2002; Cavender-Bares et al. 2009 cited in Lewinsohn et al 2005). For insect herbivores, it has been assumed over many decades that host choice is strongly influenced by the evolutionary conservatism of chemical, morphological, ecological, and physiological plant traits affecting their fitness (Weiblen et al. 2006), and closely related plant species are more likely to share the same herbivore species (Gilbert et al. 2012). Indeed, Ødegaard et al. (2005) and Weiblen et al. (2006) considered that plant phylogenetic relationships explained herbivore-host selection behaviour in tropical forests. However, Gilbert and Webb (2007) were the first to show empirically a general tendency for plant herbivores to attack closely related hosts.

Plant phylogenetic relatedness has been considered when assessing the potential consequences of intentional introductions of biological control agents into a new area. Testing the host specificity of a potential biological control agent has been widely used for risk assessment, particularly to determine the risk the agent may pose to non-target native or economically important plants in the proposed area of introduction (Schaffner, 2001; Littelfield and Buckingham, 2004). Risk assessment for biological control agents assumes that plant species that are closely related to the known hosts of the herbivore species of interest are more likely to be attacked by the new introduction (Hogg et al. 2016). Therefore, laboratory host-specificity testing has been compulsory since the 1970s worldwide and, since 1974, many biocontrol practitioners have followed Wapshere's (1974) centrifugal phylogenetic method to select test plants for candidate control agents (Brise, 2005). This method puts emphasis on intensive testing of local non-target species in the same genus as the target hosts, and less intensive testing of

non-target species at greater phylogenetic distances, according to Gilbert and Webb (2007). When empirical data is unavailable, phytosanitary agencies have followed this reasoning and have developed some phylogenetic rules-of-thumb for risk assessments (Gilbert et al. 2012). They suggest a potential species may be considered a threat if it has been recorded on a plant species of the same genus as local species of concern (APHIS 2005). Moreover, a pest species is considered of low concern if it only attacks species within a single genus, medium if it is limited to a single family and high if it attacks multiple families (PPQ 2003).

Blomberg and Garland (2002) in their review of the meaning and significance of the concept of 'phylogenetic inertia' in evolution, described phylogenetic relatedness as a "phylogenetic signal", defined as 'the tendency for related species to resemble each other more than those drawn at random from the same phylogenetic tree'. Gilbert and Webb (2007) provided a quantitative assessment of phylogenetic signal in the host range of plant pathogens by experimentally inoculating multiple host plants with pathogens in a nursery, and in a natural forest community. They confirmed in both cases that the phylogenetic signal in host range of plant pathogens can be used to assess risks from potential biological invaders including quarantine pests and pathogens.

Gilbert et al. (2012) studied crop pests as well as pathogens and further confirmed the value of using phylogenetic distance among plant species as a tool for phytosanitary risk analysis by measuring the strength of the phylogenetic signal in the host range of nine major groups of pests and pathogens. They recommended using phylogenetic distance between the known hosts of the target pest and the plant community of the target region to predict likely hosts in the new area. Moreover, Gilbert et al. (2015) recently demonstrated that the impact of those plant enemies on different plant species also shows a strong phylogenetic signal.

The phylogenetic signal between plants has also been used to improve forest management to reduce vulnerability to pest outbreaks, but also to understand the mechanisms by which biodiversity can provide resistance to pests (Castagneryol et al. 2014). Associational resistance was defined by Jactel and Brockerhoff (2007), as the reduced risk of insect herbivory of an individual plant resulting from an increase in plant community diversity and its associated predator and parasitoid species richness due to changes in host density and non-host volatiles. Jactel and Brockerhoff (2007) found that mixed forests suffer significantly less herbivory than single species forests. Based on the Jactel and Brockerhoff (2007) findings, Castagneyrol et al. (2014) showed that the relationship between tree phylogenetic diversity and herbivory varied with feeding specialization, and suggested that associational resistance increases with the phylogenetic distance between hosts and associated tree communities. Both Jactel and Brockerhoff (2007) and Castagneyrol et al. (20014) based their analysis

on meta-analysis of several studies that investigated the effects of forest diversity on insect herbivory. Both studies stated that mixed forests present more benefits than monocultures in terms of productivity, as well as greater biotic resistance to herbivory and in general, multi-functionality.

In New Zealand, host phylogenetic affinities have been used to test the host-specificity of potential biocontrol agents to minimize any risk they might pose to non-target plants (Fowler et al. 2000). As have many other biocontrol practitioners, New Zealand researchers have also followed Wapshere's (1974) approach to test the host-specificity of potential agents, for example for the heather beetle, *Lochmaea suturalis* (Fowler et al. 2000). Moreover, for a non-plant example, phylogenetic similarity between herbivores has also been used in New Zealand for assessing risks of introducing parasitic wasps as biocontrol agents. For example, Avila et al. (2016) in a study of the behavioural attraction of the parasitic wasp *Cotesia urbae* towards non-target host insects and also their host plants, the authors selected non-target species from a family closely related to the family of the target insect hosts. Moreover, host phylogenetic affinities between New Zealand and other biogeographic regions have been used to test potential treats to natural ecosystems. For example, Barratt et al. (2016) tested the Argentine stem weevil, *Listronotus bonariensis*, as a threat to New Zealand natural grassland ecosystems by determining the impact of this pest species on New Zealand native grasses that are in the same genera as species found in the weevil's native alpine ecosystems. However, to my knowledge, phylogenetic signal as a quantitative approach has never been used in New Zealand to assess the risk of introduction of biological control agents or non-native species.

New Zealand flora includes many unique species in its natural ecosystems. Large tracts of native forest are included within many national parks as well as in less well protected areas. There are also many culturally important iconic species. New Zealand's biosecurity system has the mandate to protect the country's biological resources and heritage, and must assess biosecurity risks to all of its ecosystems. One of the most difficult tasks is to assess the threat that non-native herbivores and plant pathogens pose to New Zealand's native plant species.

The aim of this study was to apply the concept of phylogenetic signal to predict if non-native herbivore invertebrates could find host plants in New Zealand natural ecosystems. Here, I determine the strength of the phylogenetic signal within the New Zealand host plant ranges of herbivore species from the Insecta, Adenophorea (a class of Nematodes) and Arachnida (mites), using representatives from these three taxa that are already established in New Zealand as non-native species. To assess differences between insect orders, I conduct a second analysis of non-native insects in New Zealand from the orders, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Thysanoptera. I then use the phylogenetic signal to predict non-native Coleoptera species likely to find host plants amongst NZ's

native flora should they become established here. For those species likely to feed on New Zealand native plants, I determine which of those plants are likely to be more susceptible by looking at the phylogenetic distance between the Coleoptera species known hosts and New Zealand natives.

4.2 Methods

4.2.1 Databases

New Zealand non-native herbivores (NZNH)

Two databases were used in this research. The first was an updated version of the Plant-SyNZ (2011) database described by Martin and Paynter (2014), which comprises approximately 570 species of non-native phytophagous arthropods, molluscs and nematodes and their host plants in New Zealand. This database is used in this study to determine the strength of the phylogenetic signal within the New Zealand host plant ranges of herbivore species contained in the database. Previously, in a study of risks presented by non-native invertebrate herbivores to New Zealand indigenous plants, Martin and Paynter (2014) used the Plant-SyNZ database as a source of previously unpublished herbivore-plant associations to compile the NZNH. They included only those associations for which evidence comprising published research or unpublished observations from field or laboratory experiments were available. They also consulted domain experts for additional information on herbivore species and their host plants in New Zealand, and checked international databases for information on the species' host plant ranges. The Plant-SyNZ database is available from http://plant-synz.landcareresearch.co.nz/adventive_herbivores.asp. While the NZNH database (Martin and Paynter 2014) includes host information for the 570 non-native species, of which I used only 561 for the host phylogenetic distance analysis within the classes Insecta, Adenophorea and Arachnida, and 443 for a separate analysis of differences between non-native insects within the orders, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Thysanoptera. The reason for the omission of some taxonomic groups included in the NZNH database, is that they comprised fewer than 10 species.

Following the Gilbert et al. (2012) methodology, herbivore records within a genus were grouped as a conservative test of phylogenetic signal. The authors assumed that if a herbivore occurs on a plant species in a particular genus, all species that comprise the genus are potentially susceptible. Gilbert et al. (2012) state that this approach provides the maximum information about phylogenetic signal at further phylogenetic distances, especially when host ranges are poorly known. The records of 613 plant genera in New Zealand for all the non-native herbivore species studied were also extracted from the Plant-SyNZ database.

Potential pest species using the Global Pest and Disease Database (GPDD)

Coleoptera species recorded in the Global Pest and Disease Database (GPDD) (maintained by the United States Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine Division [USDA APHIS-PPQ]) (Magarey et al. 2009), were used to identify the potential that coleopteran species could find hosts among New Zealand native plants (following research described in Chapter 2). The GPDD is a compendium of over 3,100 pest species of agronomic importance that are currently not present in the United States (US), or have restricted US distributions (https://www.gpdd.info/) (Gilbert et al. 2012). The database contains host plant records of each species that have been gathered from publications, compiled lists, databases, border interceptions, pest surveys, pest and commodity risk assessments, and publicly available source material (Gilbert et al. 2012). For this current study, access was obtained to the Coleoptera pest-host records that had been recorded up to January 2015, which included host plant information for 266 Coleoptera species on 298 plant genera.

Non-native coleoptera species that have potential host species within New Zealand native plants

To determine which Coleoptera species from the GPDD database are more likely to feed on New Zealand native plants, and therefore which native plants are potentially more vulnerable, a list of all New Zealand native plant genera were required. These data were extracted from the Germplasm Resources Information Network (GRIN) database (http://www.ars-grin.gov/) accessed in June 2015) (see Chapter 3 for further details of the methods).

Assumptions and limitations of the database

Databases can be subject to epistemic and linguistic uncertainties (Regan et al. 2002; McGeoch et al. 2012). Linguistic uncertainty comes from our natural language, and even scientific vocabulary can be inexact (Regan et al. 2002). Epistemic uncertainty is associated with the knowledge of a system, particularly lack of knowledge, or insufficient data. For databases of invasive non-native species, epistemic uncertainty can arise from species misidentifications and data entry errors (e.g., incomplete data) (McGeoch et al. 2012). Additionally, epistemic uncertainty will arise when there is insufficient survey information about the species of interest, or, alternatively, the data is not accessible (McGeoch et al. 2012).

Uncertainty may be problematic if its effects are ignored (Gould et al. 2014), and some sources can be reduced or eliminated, but it will always be present (Burgman, 2001). In this study, epistemic uncertainty was reduced by correcting errors in both databases. Specifically, herbivore-host relationships incorrectly listed were identified in those cases when they were listed more than once because synonyms were used. Other errors of data entry, such as misspelling were corrected. With

respect to survey bias, although it was assumed that bias was larger in the GPDD database than in the NZNH database, because NZNH authors focussed on identifying non-native invertebrate herbivores feeding on native New Zealand plants, those differences did not alter the methods or interpretation of the results.

4.2.2 Statistical analysis

The Gilbert et al., (2012) procedure was followed for using phylogenetic signal to assess phytosanitary risk. For each herbivore species in each database, a host plant genus was randomly selected from all genera on which the herbivore had been reported feeding and assigned as the 'source' host. There were 612 plant genera in NZNH and 297 in GPDD. The host plant records were then used to assign all other plant genera ('target' genera) in the databases as susceptible or resistant to that herbivore. As in Gilbert et al. (2012), each plant genus was scored 1 if the herbivore species had been recorded feeding on at least one of its constituent species, thus assuming that all species in the genus are susceptible. For each herbivore, plant genera were scored 0 when there were no records of the herbivore feeding on any species in that plant genus, thus the whole plant genus was assumed resistant. The phylogenetic distances from source to target genera were calculated from the hand-constructed supertree R2G2_20140601 (Parker et al. 2015), which, according to Gilbert et al. (2015), includes a topology of phylogenetic relationships of all vascular plant families, as well as within-family substructure for all major families of plants for which accepted topologies were available. I used the Phylomatic version included in Phylocom v4.2 (Webb et al. 2008) to create a separate pruned ultrametric tree for all plant genera in each of the databases. For each tree, the function *phydist* in Phylocom was used to calculate the pairwise phylogenetic distances in millions of years (My) for each pair of 'source' and 'target' host plant genera.

I followed the statistical procedures of Gilbert et al. (2012), which were based on Gilbert and Webb (2007). A logistic regression was used to determine the probability that closely related plant genera would share the same herbivores. For the regression, the response variable was the assumed susceptibility of the 'target' plant genus. The independent variable was the phylogenetic distance between each source and target plant genus [transformed as $\log_{10}$(phylodistance + 1)]. Herbivores limited to a single host genus were excluded to avoid intra-generic comparisons because their inclusion would force the intercept through 100% probability of sharing a host species (Gilbert et al. 2012). The logistic regression was repeated 1,000 times, using new random selections of 'source' plant hosts for each herbivore each time. All 1,000 sets of intercept and slope coefficients were recorded. The median intercept and slope coefficients and the 95% confidence interval for these coefficients across all repetitions were calculated. As in Gilbert et al. (2012), if the 95% confidence interval of a coefficient did not include zero, it was considered significant. Predicted probabilities of host species sharing a

common herbivore in intervals of 5-My (millions of years) were recorded for each of the 1,000 models. The 0.025, 0.5, and 0.975 quartiles were then calculated as well as the 95% confidence intervals of the coefficient of the curves for its further visualization.

Gilbert et al. (2012) showed that the likelihood that closely related plant species will share a herbivore increases with the number of known hosts for that herbivore. I therefore tested whether a combination of phylogenetic distance between host genera and the number of known host genera would improve predictions of the likelihood that two host genera would share a particular herbivore species, thus a subsequent set of logistic regressions was run. This analysis was also repeated 1000 times, the intercept and slope coefficients recorded, and their 95% confidence intervals calculated. Logistic regressions were completed using the statistical software R version 3.3.0 (R Core Team 2013), with functions from the R packages *plyr* v. 1.8.3 (Wickham, 2011), *data.table* v. 1.9.6 (Dowle et al. 2015), and *reshape2* v. 1.4.1 (Wickham, 2007).

Both sets of logistic regressions were calculated for the Insecta, Adenophorea and Arachnida, and for the different orders of Insecta (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Thysanoptera) in the NZNH database. Finally, the logistic regression relating the susceptibility or resistance of host plants to the Coleoptera herbivores in the GPDD database to phylogenetic distances in their host range was calculated. This last analysis was used to predict which non-native Coleoptera species would be more likely to feed on New Zealand native plants, and which New Zealand native plants would be more likely to be susceptible.

4.3 Results

4.3.1 Phylogenetic signal in host ranges of selected non-native phytophagous taxa in New Zealand

The probability that two plant genera will share a herbivore declined significantly with phylogenetic distance between source and target plant genera for the three taxonomic classes (Insecta, Adenophorea and Arachnida) as well as the different insect Orders (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Thysanoptera). For each herbivore taxon, the regression curves took the form of exponential decays (slope (β_1) defines the decay rates) and the 95% confidence interval did not include zero (Table 4.1).

Table 4.1 Phylogenetic signal in herbivore sharing between plant host genera.

	Coefficients		95% confidence intervals	
Organism class (n)	β_0	β_1	β_0	β_1
Adenophoera (38)	1.9077	-1.9218	1.8891 to 1.9263	-1.9297 to -1.9140
Arachnida (79)	2.7093	-2.5222	2.6745 to 2.7441	-2.5372 to -2.5071
Insecta (444)	2.2319	-2.8208	2.2224 to 2.2414	-2.8251 to -2.8165
Insect order (n)	β_0	β_1	β_0	β_1
Coleoptera (79)	3.0095	-2.7981	2.9867 to 3.0322	-2.8083 to -2.7879
Diptera (29)	6.8709	-3.9628	6.7662 to 6.9755	-4.0099 to -3.9156
Hemiptera (231)	2.3192	-2.6743	2.3039 to 2.3344	-2.6810 to – 2.6676
Hymenoptera (27)	7.1863	-4.7991	7.0950 to 7.2776	-4.8449 to -4.7532
Lepidoptera (61)	3.2501	-2.9359	3.2234 to 3.2768	-2.9481 to -2.9237
Thysanoptera (16)	3.1040	-2.3780	3.0628 to 3.1452	-2.3968 to -2.3593

Coefficients of logistic regressions (median and 95% confidence intervals) of target host plant genus susceptibility (S) to an herbivore as a function of the phylogenetic distance between source and target hosts. The regression takes the form of logit(S) = $\theta_0 + \theta_1 * log_{10}(PD + 1)$, where PD is the phylogenetic distance (time of independent evolution in My) between the source and target host genera (Gilbert et la. 2012). Phylogenetic signal was considered significant when 95%CI for θ_1 did not include 0. And the intercept (θ_0) is the expected mean value of Y when all X = 0.

From the analysis of the three taxonomic classes of organisms (Table 4,1, Figure 4.1), the Insecta shows the steepest slope (β_1 =-2.82) and a small intercept (β_0 = 2.2319) indicating a high sensitivity to host phylogenetic distance, while the nematode taxon (Adenophorea) has the shallowest slope (β_1 =-1.9218) but the smallest intercept (β_0 = 1.9077). As a result, nematodes appear to be much less sensitive to phylogenetic distance than insects. Differences between the slopes for each taxon also have non-overlapping confidence intervals indicating differences that are likely to be significant. Of the insect orders, while Hymenoptera and Diptera have the steeper slopes (Table 4.1), they also have the highest intercepts. As a result, they have broader host plant ranges than Coleoptera, Hemiptera and Lepidoptera, which have shallower slopes and much lower intercepts. Thysanoptera on the other hand, despite having a shallow slope and a low intercept, appears to have a broad host plant range according to the predictions, which contrasts with the results of all the other groups (Figure 4.1).

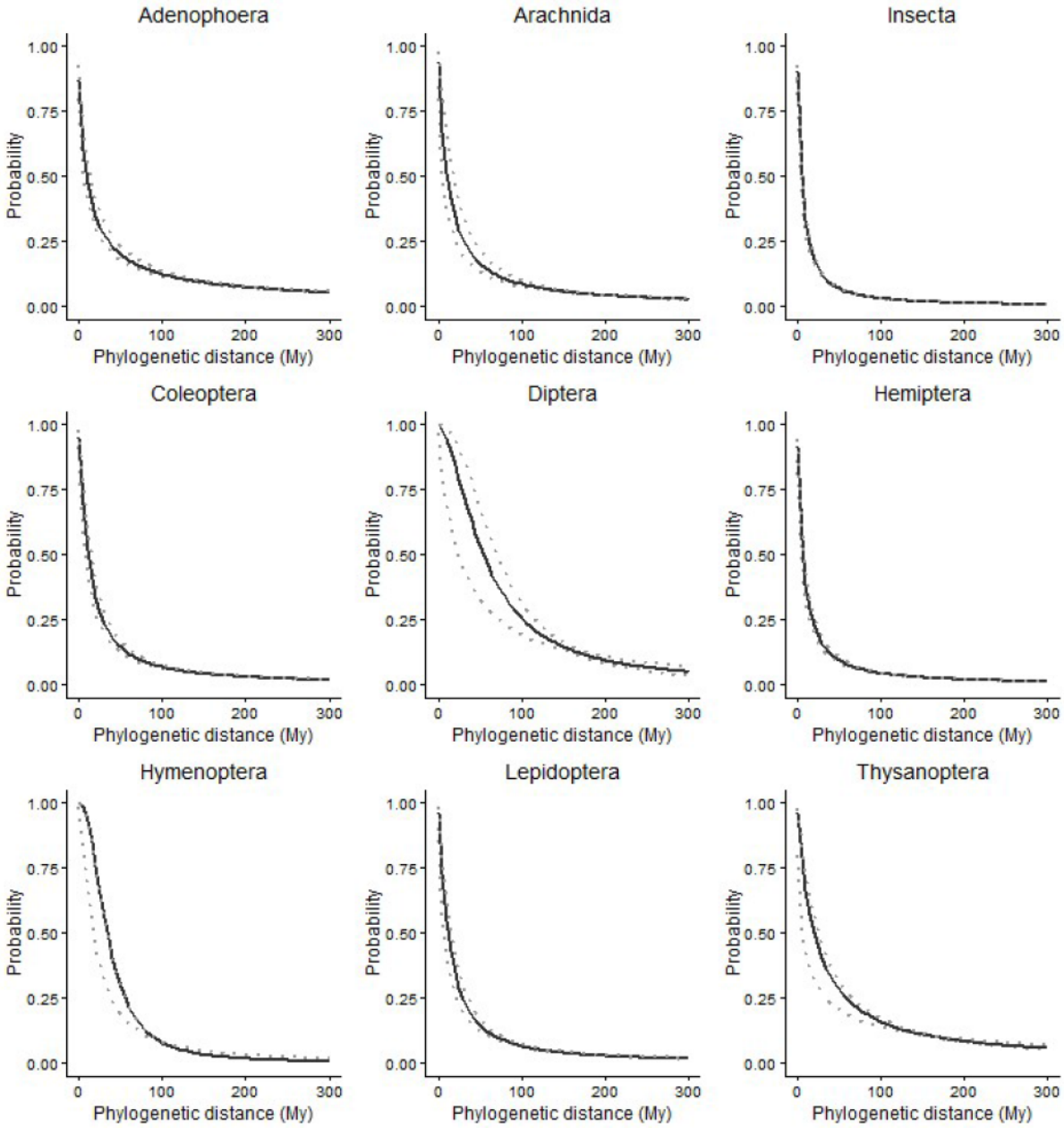


Figure 4.1 Logistic regressions for the probability of sharing herbivore species against phylogenetic distance between source and target plant genera. Dashed lines represent the 0.025 and 0.975 quartiles, while the solid line represents the 0.5 quartile.

4.3.2 Interaction between host breadth and phylogenetic signal

The results indicated that herbivores with more known host plant genera would be more likely to have a wider host range across all plant phylogenetic distances (Table 4.2 and Figure 4.2). The interaction between the number of known host plant genera and phylogenetic distance between host plant genera was significant for all classes of organisms, (see Appendix C.1). In both models, the one just including the main effects of the phylogenetic distance and the number of hosts and the model including also the interaction, the two main effects are significant.

Table 4.2 Effect of host range and phylogenetic distance on the likelihood the two hosts share a herbivore.

	Coefficients			95% confidence intervals		
Organism class (n)	β_0	β_1	β_2	β_0	β_1	β_2
Adenophoera (38)	1.3462	-2.2167	0.1009	1.3261 to 1.3663	-2.2259 to -2.2075	0.1008 to 0.1009
Arachnida (79)	2.6521	-2.8581	0.0402	2.6257 to 2.6785	-2.8696 to -2.8465	0.0402 to 0.0403
Insecta (444)	1.9340	-3.0079	0.0414	1.9239 to 1.9441	-3.0127 to -3.0032	0.0413 to 0.0414
Insect order (n)	β_0	β_1	β_2	β_0	β_1	β_2
Coleoptera (79)	2.4676	-2.9837	0.0916	2.4470 to 2.4882	-2.9933 to -2.9741	0.0915 to 0.0916
Diptera (29)	6.4737	-4.5031	0.1315	6.3755 to 6.5721	-4.5487 to -4.4575	0.1309 to 0.1321
Hemiptera (231)	1.9709	-2.8868	0.0389	1.9561 to 1.9859	-2.8938 to -2.8799	0.0389 to 0.0389
Hymenoptera (27)	5.8425	-4.6424	0.0788	5.7804 to 5.900	-4.6707 to -4.6142	0.0785 to 0.0788
Lepidoptera (61)	2.5807	-3.1245	0.0903	2.5546 to 2.6068	-3.1365 to -3.1125	0.0897 to 0.0908
Thysanoptera (16)	2.9693	-2.9588	0.2252	2.9376 to 3.009	-2.9764 to -2.9412	0.2228 to 0.2276

Coefficients of the logistic regression (median and 95% confidence intervals) of phylogenetic signal in host sharing using two independent variables: phylogenetic distance between source host plant genus and target host plant genus (coefficient θ_1) and the number of known host plant genera for each herbivore (coefficient θ_2), plus the intercept (θ_0). The independent variable was whether the target host plant genus was susceptible (S) or resistant to a herbivore in the source host plant genus. The regression takes the form of logit(S) = $\theta_0 + \theta_1 * \log_{10}(PD + 1) + \theta_2 *$(number of known hosts), where PD is the phylogenetic distance (time independent evolution in My) between the source and target host genera (Gilbert et al. 2012).

When the interaction between the two independent variables was omitted, the coefficients for phylogenetic distance were significantly negative indicating that the probability of sharing a herbivore decreases with the phylogenetic distance of the plant species, and the coefficients for the number of known hosts were significantly positive in both models indicating that the probability of sharing an herbivore increases with the number of known hosts of the herbivore species studied (Table 4.2 and Figure 4.2). However, when the interaction was included, the coefficients for the number of known hosts were significantly positive for all taxonomic classes, except for insects when analysed by class, which were negative (see Appendix C.1). However, when insects are divided by orders, for the models including the interaction, the coefficients were significantly positive.

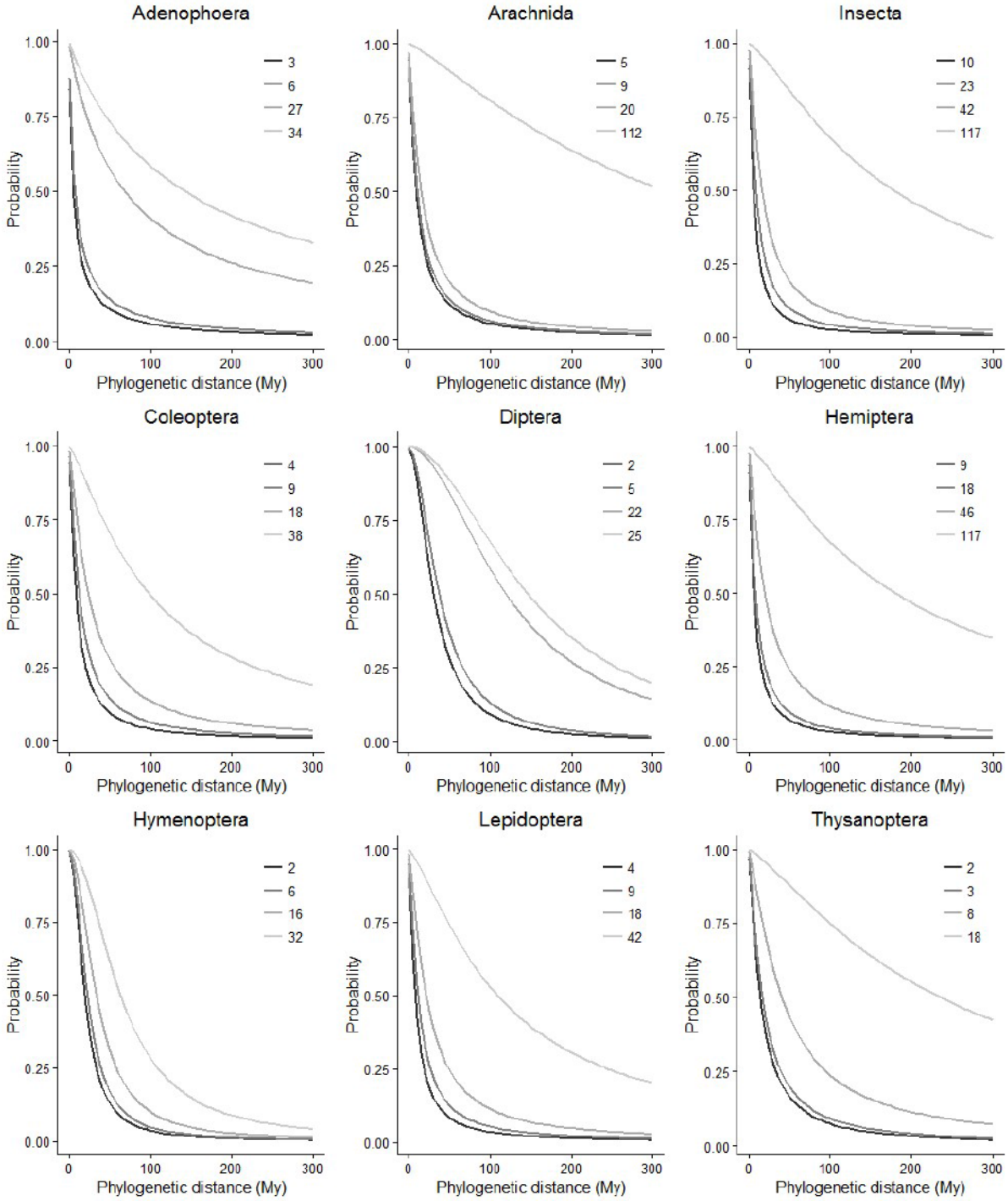


Figure 4.2 Logistic regressions for the probability of host plant genera sharing herbivore species with phylogenetic distance and number of known hosts as independent variables. The probability that all herbivores or pathogens from one host genus ('source') will also be found on another host genus ('target') can be calculated using the phylogenetic distance between the source and target host genera, and the number of known hosts of the herbivore, and parameterized using the coefficients given in Table 2, as follows: $\text{logit}(S) = \beta_0 + \beta_1 * \log_{10}(PD + 1) + \beta_2 *(\text{Number of known hosts})$, where prob('target' is susceptible) = $\exp(\text{logit}(S)) / [1 + \exp(\text{logit}(S))]$.

4.3.3 Coleoptera that threaten New Zealand native plants

A logistic regression between host plant genus susceptibility to herbivory and phylogenetic distance between source and target host plant genera for herbivorous Coleoptera species was used to determine which herbivores from the GPDD database would be more likely to feed on New Zealand native plants, should they become established there. This association was also used to predict which New Zealand native plants are more likely to be used as hosts by Coleoptera species in the GPDD database.

According to the results, 54 native New Zealand plant genera could be hosts, and 96 Coleoptera species have a probability > 0.1 (when the probability generally reaches an steady state or plateau) of expanding their host range from their known host range to a New Zealand native plant. The New Zealand native plant genera were ranked according to the number of herbivore species that could feed on them and the probability that they may be susceptible (see Appendix C.2). The plant genera that have the highest probabilities of sharing a herbivore are those on which a herbivore has at least one recorded host from the same genera. The genera are *Solanum*, *Apium*, *Dacus*, *Ipomoea*, *Sicyos*, *Rubus*, *Linum*, *Aristotelia*, *Nothofagus*, *Sophora*, *Dysoxylum*, *Hypericum* and *Lythrum*.

Ninety-six herbivore species were ranked in a list based on the number of potential hosts that are present in the New Zealand flora and the probability of expanding their host range to those plants (higher than 0.1, see Appendix C.3). Five of the 96 species are already established in New Zealand (*Heteronychus arator*, *Epilachna vigintioctopunctata*, *Naupactus leucoloma*, *Amasa truncata* and *Phoracantha semipunctata*). Four have already been recorded feeding on New Zealand native plants, with the exception of *P. semipunctata* (Plant-SyNZ 2015). One species of the 96, *Costelytra zealandica*, is native to New Zealand, where it has become a pest of exotic pastures (Lefort et al. 2014). Moreover, eleven out of the 95 non-native herbivores have another non-native species of the same genus already established in New Zealand (*Naupactus xanthographus*, *Bruchus tristis*, *Otiorhynchus armadillo*, *Otiorhynchus ligustici*, *Lema bilineata*, *Epilachna varivestis*, *Acanthoscelides obvelatus*,, *Bruchidius tristis*, *Bruchidius atrolineatus*, *Phoracantha recurve*, *Phoracantha semipunctata* and *Scolytus intricatus*), but just two of these genera of herbivore species, not in the GPDD database have been recorded feeding on New Zealand native plants (*Naupactus xanthographus* and *Epilachna varivestis*) (Plant-SyNZ 2015).

4.4 Discussion

My results demonstrated that, as expected, the host ranges of the non-native herbivore species established in New Zealand, studied here, are influenced by plant phylogenetic affinities. Interestingly, the probability of feeding on new host plants, and therefore the phytosanitary risk associated with the

species, varies among the classes of herbivore taxa and among the orders of phytophagous insects. Including the number of hosts of the herbivore species considered in this study with phylogenetic distance between hosts in the models makes interpretation more clear. Thus the probability of two plant genera that do not initially appear to be closely related, sharing a herbivore species, was higher for herbivore species with a greater number of host plant genera (Figure 4.2), as demonstrated by Gilbert et al. (2012). Moreover, the results suggest that herbivores with a large number of host plant genera, are likely to have a broader host range that is likely to include a number of unreported host plants. The reason is that herbivore-host databases are subject to inherent assumptions (discussed below) that could systematically bias results of studies of the host range of herbivore species as well as the number of species on a particular host (Gilbert et al. 2012).

It has been argued that many herbivore surveys have a strong bias toward plants important in agriculture, horticulture and forestry and that coverage of native species that are not cultivated is much more limited (Gilbert and Webb, 2007; Gilbert et al. 2012). The reason is that many herbivore species that are studied are generally those with an imminent or realized economic impact, which is difficult to quantify for species in natural ecosystems that are not used for production purposes and where invaders are also less frequently observed (Goodell et al. 2000). Moreover, often only plant susceptibility is recorded and records of plant resistance are rarely included in herbivore-host databases which can lead to many false negatives (Gilbert and Webb, 2007; Gilbert et al. 2012). Thus, results from inaccurate or incomplete databases can give misleading results. As explained in the Methods section of this chapter, NZNH authors (Martin and Paynter 2014) attempted to reduce the survey bias by gathering non-native species records on New Zealand native plants; however, only plant susceptibility was recorded. Furthermore, the uncertainty around true resistance of New Zealand native plants is increased by the lack of knowledge on New Zealand natural ecosystems, where many herbivore-plant interactions have not been described yet. Moreover, it is thought that many native invertebrate species are still undescribed, thus it is sometimes uncertain if a new species is a New Zealand native or a new invader.

Despite the potential influence of survey bias on my results, a likely interpretation is that nematode species might represent a greater risk than insects and arachnids because they have a broader host range but also because they feed on less closely related species, based on the logistic regression analysis (Table 4.1 and Figure 4.1). Nevertheless, insect species, when analysed as a class, seem to feed on less closely related plants and have a narrower host range, whereas, when analysed at the order level, they show more risk variability based on the probabilities estimated from the logistic regression analysis (Table 4.1 and Figure 4.1). With regard to the insect orders studied, Thysanoptera and Diptera show a broader range of potential hosts and they feed on less closely related plants according to the

relationship of the probability of sharing a host and the phylogenetic distance between 'target' hosts (Figure 4.1). Thus, these two insect orders might present a greater phytosanitary risk for New Zealand. Based on the same relationship (Figure 4.1), Hemiptera species are likely to have a narrower range of closely related plant species. Differences between the groups of organisms studied need to be interpreted with caution because the probabilities estimated represent an extrapolation beyond the range of data used to parameterize the models, which assumes that trends observed will not change over time due to new herbivore-plant interactions (Gilbert et al. 2012). Therefore, my results are likely to be influenced by the number of non-native herbivorous species in my samples, which, if too small, may not provide enough statistical power. For example, Diptera, Hymenoptera and Thysanoptera were the groups with fewest species (see Table 4.1) and also the groups that seem to represent greater phytosanitary risk, according to my predictions (Figure 4.1).

However, even when the sample size is large, for example in the insect order Hemiptera, the combination of the number of hosts and the phylogenetic distance between plants may not be enough to indicate the potential risk for feeding on New Zealand native plants. In this case, my results contrast with findings of previous studies, particularly with Martin and Paynter (2014). Martin and Paynter (2014) analysed the risk to New Zealand indigenous plants by testing the proportions of different taxonomic groups of mites and insects established in New Zealand that feed on indigenous plants. They showed that for New Zealand indigenous plants in particular, Hemiptera species represented the greatest risk because of their broad host range and the large number of records of species feeding on indigenous plants. Martin and Paynter (2014) also analysed the importance of the host range breadth by testing the proportion of polyphagous, oligophagous and monophagus species and their occurrence on native plants. For their research, Martin and Paynter (2014) used a previous, 2013, version of the NZNH database. Within the non-native species considered in the 2013 version of the database, Martin and Paynter (2014) found that Coleoptera, Hemiptera and Thysanoptera comprised the highest proportions of the total number of phytophagous species (40%, 41% and 45% respectively) established in New Zealand. In accordance with the Martin and Paynter (2014) findings, Ridley et al. (2000) also found that most of the non-native species feeding on New Zealand native plants are sapsucker species (Hemiptera) with a broad host plant range. In a report to assess the likelihood and consequences of non-native pests and pathogens in New Zealand native ecosystems, Ridley et al. (2000) related feeding guild and the degree of host specificity with successful establishment and impact on New Zealand native plants. Thus, it would be expected that feeding guilds that circumvented plant defences, such as most wood borers which feed on dead material, and phytophagous sapsuckers which avoid 'green cell' defence systems by directly feeding in the photosynthate stream, are more likely to find suitable hosts among the highly endemic New Zealand flora. However, my results relating plant susceptibility and 'target' host phylogenetic distance suggest that Hemiptera species are likely to feed on a narrow

range of closely related plant species. In fact, the probability of two plant species sharing Hemipteran herbivore species decreases more rapidly with the increase of the phylogenetic distance between plants than for other insect classes (Figure 4.1). The exception is Hemipteran species that have a large number of known host species, about the 10% of the species studied (Figure 4.2).

A potential explanation for the differences between my results and the observations of Martin and Paynter (2014) of actual herbivore-plant relationships is that my models are likely to be strongly influenced by the large number of relatively host specific (oligophagous) Hemiptera, therefore my predictions can be strongly biased by their closely related host plant genera. Other studies suggest that the influence of host phylogenetic affinities to explain herbivore-plant interactions varies depending on the level of host specificity of herbivores (e.g., Castagneyrol et al. 2014). However, host specificity can show a spatial turn over, thus a particular species can show high specificity at local scale while being generalist on a global scale or vice versa (Poulin et al. 2011). Therefore, host specificity based on one locality (α-specificity), host affiliations among localities (β-specificity), or over the entire geographical range of a species (γ-specificity) are likely to be different. An example of this geographic variation in host usage is the Colorado potato beetle, *Leptinotarsa decemlineata*, whose regional Mexican populations are rather diet restricted to *Solanum rostratum*, but globally it feeds on a wide range of both wild and cultivated host plants in the genus *Solanum* (Horton et al. 1988; Izzo et al. 2014). The Colorado potato beetle evolved after being unintentionally introduced first in North America and then in Europe, and expanded its host range to suitable host plants (Horton et al. 1988; Izzo et al. 2014; Cingel et al. 2016). Colorado potato beetle is considered a fairly restricted feeder to cultivated and wild *Solanaceae*, and for that reason intraspecific geographic variation seems to be influenced by the phylogenetic relations between plants. Therefore, the importance of the phylogenetic distance between plants and its relation with the degree of host specificity of the species at different geographic scales needs further investigation.

Despite these caveats, my results support the use of a phylogenetic signal as a reasonable approach for predicting the likelihood of coleopteran herbivores feeding on New Zealand native plants when empirical data is limited. The results indicate which native New Zealand plant genera are more likely to be susceptible to Coleoptera species recorded in the GPDD database, particularly if their known host range contains plant species of the same genus as New Zealand native plants. As a validation of the importance of the host phylogenetic signal for phytosanitary risk analysis, my list of herbivores potentially affecting New Zealand native plants includes five species that have actually been recorded feeding on New Zealand native plants (see results section "Coleopteran threats for New Zealand native plants" and Table S3). The other species listed could be considered likely to feed on New Zealand native plants, provided that other biotic and abiotic factors are favourable for their establishment in New

Zealand. Of the five non-native species already established in New Zealand, the African black beetle *Heteronychus arator* is a sporadic but serious herbivore of pasture in northern areas of the North Island (King and Watson 1982; Wilson et al. 2016), but it has also been recorded feeding on leaves of the New Zealand native *Solanum aviculare* (Martin 1999). The hadda beetle, *Epilachna (Henosepilachna) vigintioctopunctata* is now considered established in New Zealand after small populations were first detected in 2010 in parts of Auckland. This species has subsequently been found to be more widespread and feeding on several *Solanum* species (Plant-SyNZ 2015). The white fringed weevil, *Naupactus leucoloma*, is known to be highly polyphagous (Lanteri et al. 2013) and it has been found in New Zealand feeding on a range of plant species in improved pastures (Hardwick 2004), but also on the native *Solanum aviculare* (Martin 1999). Finally, the non-native wood borer *Amasa truncata* (syn. *A. truncatus*) feeds on dead exotic and native New Zealand trees, but also on live eucalyptus (Brockerhoff and Bain 2000). With respect to New Zealand native trees, broods of *A. truncata* were found particularly *on Kunzea ericoides*, *Leptospermum scoparium*, *Knightia excelsa*, *Metrosideros robusta*, *Metrosideros excelsa*, and *Weinmannia racemosa*, as well as adults boring in *Prumnoptys taxifolia* (Brockerhoff and Bain 2000). Records of these four non-native species discussed here suggest that *Solanum* is one of the genera of New Zealand native plants with more risk of being attacked by non-native beetle species, since three of the already established species feed on this genus.

The use of phylogenetic signal between plants is a useful tool to identify threats to native ecosystems from phytophagous insects, although it is important to recognise that the results represent an extrapolation beyond the range of data used to parameterise the models. Thus, the models are likely to be biased due to variation in the quantity and quality of that data, as previously discussed. Moreover, Gilbert et al. (2012) demonstrated that the slopes for phylogenetic signal coming from pest-host databases were usually steeper than those found in empirical host range tests in earlier work by Gilbert and Webb (2007). One of the reasons for those differences was that Gilbert and Webb (2007) had limited empirical data. They restricted their analysis to pathogens that easily grow under laboratory conditions. Moreover, both the pathogens and plants occurred in small geographical areas with limited number of potential hosts, and also that the host range that Gilbert and Webb (2007) tested was intentionally phylogenetically broad.

Due to the uncertainties of extrapolation and potential differences with empirical host range tests, I recommend to use this tool as a filter for more detailed risk assessments. Thus, host phylogenetic affinities could be added to other factors such as propagule pressure, climate matching (Williamson 1996; Leung et al. 2012) and plant similarity (Chapter 3) to assess the risk of establishment and invasion of non-native herbivore species. This plant phylogenetic analysis could also be useful to regulatory authorities, such as the Ministry for Primary Industries (MPI) in New Zealand, to rapidly evaluate the

host range of a newly detected invader and decide on appropriate management actions. Host phylogenetic affinities analysis can help to prioritize empirical tests and individual herbivore risk assessments on high risk-ranked herbivore species, and can therefore be used as another tool for risk assessment protocols. Further empirical tests will provide more information for the herbivore-host databases thereby reducing epistemic uncertainty by, for example, reducing the number of false negatives. Furthermore, open-field tests and samples of herbivory of non-native invertebrate species would help improve the knowledge of the effects of phylogenetic distance between plants on non-native phytophagous community assembly, as has been done for forest plantations by Castagneyrol et al. (2014). Identifying vulnerable plant communities will help prevent and manage potential non-native phytophagous establishments. Finally, future work is required to establish the influence of host specificity and the geographic scale on the phylogenetic relation between known hosts and other plants.

Chapter 5

Invasive non-native species' impact classification systems: a case study using expert elicitation

5.1 Introduction

Invasive alien species (IAS), frequently defined as the subset of alien species that have negative impacts (McGeoch et al. 2010), are considered one of the biggest threats to biodiversity (Millenium Ecosystem Assessment 2005). Their ecological impacts have been reported at different levels of biological organization and at different spatial scales (Kenis et al. 2009; Simberloff et al. 2013). Evaluating, comparing and predicting impacts of non-native species is critical for developing and prioritising mitigation measures (Blackburn et al. 2014). In particular, quantifying IAS impacts can help decision makers and managers to prioritize their efforts to regulate and manage species with the highest impact on socio-economic systems (Nentwig et al. 2010). However, in order to prioritize species, they need to be ranked, which can only be done by quantifying their impact within severity categories.

Often, impact assessments are part of more extensive risk assessments. A large literature describes the different risk assessment systems available. For example, the World Trade Organitzation in the Agreement on the Application of Sanitary and Phytosanitary Measures identified an approach to setting measures based on risk assessments (SPS Agreement, WTO 1995). The SPS Agreement identifies three steps, the second of which is to evaluate the likelihood of a species' entry, establishment and spread and associated potential consequences (Blackburn et al. 2014). However, results of impact assessments can vary between risk assessment systems (Kumschick and Richardson 2013), creating uncertainty about which to use. Moreover, the qualitative nature of impact descriptions used in assessments can lead to inconsistencies between assessors (Kumschick and Richardson 2013). Thus, many authors have attempted to create generic or unified impact-scoring system to standardize impact assessments (e.g. Nentwig et al. 2010, Sandvik et al. 2013, Blackburn et al. 2014). Most qualitative impact classification systems verbally describe the importance of the consequences of the hazard as 'severity categories', and assign point scores to various combinations of hazard probability and severity that are combined to represent the overall 'risk' (Burgman 2005). Such impact classification systems generally use estimates from multiple experts of the impacts of a species, usually based on uncertain information. While there is a large literature emphasizing the need for systematic approaches to selecting assessors, eliciting risk estimates and combining their judgements (Burgman 2005), few invasive impact classification systems propose a systematic elicitation protocol (Burgman et al. 2014). For example, Kumschick et al. (2012) developed a framework

for prioritizing IAS according to their impacts, which integrates stakeholder interests and scientific impact descriptions. However, it does not consider how cognitive psychology can introduce bias. Thus, elicitation procedures need to be designed to offset a range of predictable biases, such as experts being subject to cognitive and motivational biases that impair their ability to accurately report their true beliefs (Burgman 2005; McBride et al. 2012). Expert judgements may also be influenced by individual values and conflicts of interest, and can be sensitive to overconfidence, anchoring, halo effects, availability bias and dominance (see McBride et al. 2012 for references).

A commonly used general methodology for eliciting and encoding expert knowledge, to overcomes these limitations, is organized in four steps: identify and select the experts, elicit the information, evaluate the reliability of the information, and aggregate the information to reach decisions (Burgman, 2001; Drescher et al. 2013). Choosing experts starts by identifying multiple experts with different backgrounds so that the chance of bias towards a similar point of view is reduced. However, greater diversity could increase the level of disagreement, which needs to be communicated with the results (Burgman, 2004). Once experts have been selected, key definitions, the objectives of the research, the elicitation process and the expected outcomes need to be communicated (McBride et al. 2012; Drescher et al. 2013). Face to face meetings or workshops are generally considered more effective, although there are good examples of remote interactions, such as that reported by McBride et al. (2012), who developed a structured elicitation for threatened species assessment using email. Depending on the type of knowledge, one of several aggregation techniques can be used. First, there are behavioural approaches to create consensus among experts (Drescher et al. 2013), such as the Delphi process, which is widely used in ecology (McBride et al. 2012). Mathematical approaches can also be used to combine information, which are general based on either probability theory, or fuzzy set theory (Drescher et al. 2013). Probability theory can employ either frequentist or Bayesian approaches to combining data (Clemen and Winkler 1999 cited by Drescher et al. 2013). Once the information is combined, it can be used to reach decisions.

Even though a clearly structured expert elicitation method might improve agreement between experts on IAS impacts, due to the qualitative nature of existing impact classifications schemes, I expected that impact assessments which use such schemes will not be better than random. The aim of this study was to compare IAS impact assessments made by experts using two different impact classification frameworks to identify and understand the sources of uncertainty related to impact classification systems and help future development of robust classification schemes. Four terrestrial non-native invertebrate species established in New Zealand (some perhaps without negative ecological impacts) were chosen as case studies for assessing agreement between experts on two invasive species ecological impact classification systems. Experts were chosen and an elicitation format identified. The

Delphi approach - a two-step, anonymous and iterative survey of a panel of experts (Hawkins et al. 2015) - was used to assess agreement about the classification systems. The Delphi approach used allowed experts to refine their impact estimates based on the answers of other group members while maintaining anonymity. In this Chapter, I use the term "alien" instead of "non- native", and IAS when referring to non-native species having impacts on the ecosystems to comply with the terms used in the impact assessments reviewed here.

5.2 Methods

5.2.1 Literature review of existing impact assessments and impact classification systems

I searched the literature on IAS impact assessment tools and risk assessment systems that integrated an impact rank system. Publications listed in the ISI Web of Knowledge and Google Scholar were used, along with references cited in those publications. Combinations of the following key words were used for the literature search: 'alien', 'invasive', 'non-native', 'impact', 'classification', 'risk', 'assessment' 'scoring', 'generic' and 'unified'. Special attention was given to publications that based their ecological impact assessment system on the framework of Parker et al. (1999) to assess ecological effects of IAS, because it attempted to rank the impacts of diverse taxa on different invaded ecosystems (e.g. terrestrial, freshwater). In addition, studies assessing economic impacts of IAS, and risk assessment systems in which impact was a dominant component were also considered. See Appendix D.1 for the extensive literature review.

5.2.2 Choice of classifications

The generic impact scoring system (GISS) was a recent attempt to create a standardized tool to quantify and compare impacts among taxonomic groups and geographic regions (Nentwig et al. 2010; Kumschick and Nentwig 2010; Nentwig et al. 2016). The main aim of this scoring system was to rank IAS impacts to help prioritise management, and has been one of the most used frameworks. Since its creation, the GISS has been modified to include a range of different taxonomic groups. In this study, I focussed on two refinements of the GISS, described by Kumschick et al. (2012) and Blackburn et al. (2014) that combine published evidence with expert assessment. Kumschick et al. (2012) proposed an impact assessment framework that integrates impact scoring and stakeholder opinion, and attempts to provide a balanced view of IAS impacts by accounting for positive and negative ecological and economic impacts. Blackburn et al. (2014) proposed a framework that involves aligning the GISS and the impact scheme of the Global Invasive Species Database (GISD) implemented by the Species Survival Commission (SSC) of the International Union for Conservation of Nature (IUCN). Both Kumschick et al.'s (2012) and Blackburn et al.'s (2014) impact scoring systems were designed for similar types of experts who aim to prioritize species according to their impacts. However, Blackburn et al.'s (2014)

framework only considers deleterious ecological impacts, not economic ones. Also, it calculates the overall impact of a species as the maximum impact score in any of the mechanisms of impact, while the Kumschick et al. (2012) classification sums all the impacts. Kumschick et al. (2012) suggested that impact categories coud be weighted to accord with stakeholders' values, but this was not done in my current study. Each participant ranked all ecological impact categories, which were considered to be of equal weight. Further details are given in the Appendix D.1.

5.2.3 Choice of experts

Several authors recommend grouping multiple experts with different backgrounds to obtain a range of knowledge and perspectives. In most cases, the literature suggests larger group sizes provide better estimates of true values where, although the chance of outliers will increase with group size, the influence of outliers diminishes. Thus, Burgman, (2004) and Mukherjee et al. (2015) suggest that while increasing the number of experts can potentially increase the level of disagreement, it can be beneficial because it critically minimises potential biases through self-interest. Traditionally, experts have been chosen based on factors such as years of experience, number of peer reviewed publications in international journals, direct involvement in the issue or problem, engagement with relevant organisations, and indigenous knowledge (Mukherjee et al. 2015). However, those are often poor indicators of expert performance and can have perverse consequences such as reinforcing an expert's authority and hindering effective communication (Burgman et al. 2011). Burgman et al. (2011) therefore give several recommendations to improve expert contributions, highlighting the value of trained experts that have experience conducting risk assessments. Thus, I included previous experience with invasive species risk assessments as a criterion for selecting my experts.

Two groups of experts participated in the elicitation, one per impact classification system. Both groups included scientists (invasion ecologists and taxonomists), stakeholders (e.g. land managers, members of environmental organizations), and decision makers within national and local government agencies responsible for conservation and biosecurity. A group of nine assessed the Kumschick et al. (2012) system, and of which eight completed the full elicitation process. A group of seven assessed the Blackburn et al. (2014) system, of which five completed the full elicitation process. Just one land manager and one taxonomist participated in my study, and therefore were under represented because the majority of participants were risk analysts and invasion ecologists.

5.2.4 Species selection

The four species chosen as case studies were two generalist predators, the Australian red-back spider (*Latrodectus hasseltii*) and the common wasp (*Vespula vulgaris*), and two plant-feeding beetles, the European elm bark beetle (*Scolytus multistriatus*), which is known to be the main vector of Dutch elm

disease (Brockerhoff et al. 2006), and *Pselactus spadix*, a weevil associated with decaying marine timber (Oevering et al. 2001). Experts were asked to rank species based on their ecological impacts on New Zealand native ecosystems using one of the two previously described impact classification systems. The species varied in their mechanisms, categories (Blackburn et al. 2014) and levels of impact. Similarly, the quantity and quality of available information about these species also varied. Information on the species and their ecological effects, mainly in New Zealand, was compiled and shared with the participants before they were asked to complete the questionnaires.

5.2.5 Expert elicitation

Expert knowledge elicitation and encoding methods are commonly used to limit the subjective biases and uncertainties that negatively influence risk ranking. I was particularly interested in an iterative elicitation process that would allow the participants to reconsider their initial risk assessments, which has been demonstrated by Burgman et al. (2011) to increase their average performance. Therefore, a combination of the Delphi technique and the nominal group technique (NGT) was used following the protocol of McBride et al. (2012) and Mukherjee et al. (2015). According to Mukherjee et al. (2015), the Delphi technique and the NGT are structured iterative surveys of an expert group. All of the group's risk estimates are shown to all the experts, who have the opportunity to collectively discuss differences of opinion regarding the different impact assessments. Each expert can then review their initial assessment based on conclusions from the discussion. The Delphi technique maintains the anonymity of the participants over the complete iteration process, but the NGT is not anonymous and is therefore guided by a moderator, who asks participants to prioritize ideas and suggestions of group members (also referred to as the *estimate, talk, estimate* technique) (Mukherjee et al. 2015). Anonymity releases experts from social pressures, but can also reduce respondent accountability (Powell 2002; Landeta 2006) and lead to incorrect responses and lapses of judgement (Mukherjee et al. 2015).

In this study, an adaptation of the Delphi and NGT techniques was used. The participants gave anonymous individual estimates of the impact of each species studied for each mechanism of impact then, during the collective discussion, they chose whether to remain anonymous. Thus, answers should be carefully considered due to potential social pressures (Mukherjee et al. 2015).

Approval for the study was obtained from the Lincoln University's Human Ethics Committee and written consent was provided by all participants. Before the final elicitation, a trial of the elicitation process and methodology was conducted in a workshop with invasion ecologists. The trial helped identify and eliminate linguistic ambiguities in the questionnaires created by inadequately formulated questions (Mukherjee et al., 2015).

For the main elicitation, 33 experts were contacted by email and informed of the objectives and period of the elicitation, of which 16 agreed to participate in the project. They were randomly divided into two groups, one for each classification system, and each group was asked to give anonymous IAS impact estimates using online questionnaires (See Appendix D.2). Afterwards, the participants were provided with a statistical summary of each individual's impact scores, the frequency distribution of the scores of all the participants and measures of central tendency. These results were discussed on-line, separately for each classification, and participants chose whether to remain anonymous. After the discussion, participants were asked to reconsider their initial answers by giving a second anonymous estimate of species impact. The new frequency distributions and measures of central tendency were provided to participants, who could request additional changes to their own estimates and discuss (on-line and for each framework separately) the impact rank of the species studied.

5.2.6 Analysis of responses

To test if the assessments differed from random, agreement between experts within each group was examined. The level of agreement between experts of impact attributed to each mechanism and each species was quantified using Spearman's rank correlation coefficient (Burgman 2001). Thus, a value of 1 would indicate perfect agreement between experts, and 0 would indicate a random assortment of ranks. Spearman's rank correlation coefficient was also used to compare agreement between experts with regard to the overall impact of each species within classification systems. Correlation coefficients and medians of the coefficients were calculated using R version 3.3.0 (R Core Team 2013). Graphics were created using the R package *ggplot2* (Wickham, 2009).

5.3 Results

5.3.1 Species ranking

After the main round of the expert elicitation process, the mode of the overall impact assessment for all experts for each of the species was calculated. This measure of central tendency would normally be used to help rank the four species according their level of impact in New Zealand native ecosystems and prioritize management strategies against the species with the greater impact.

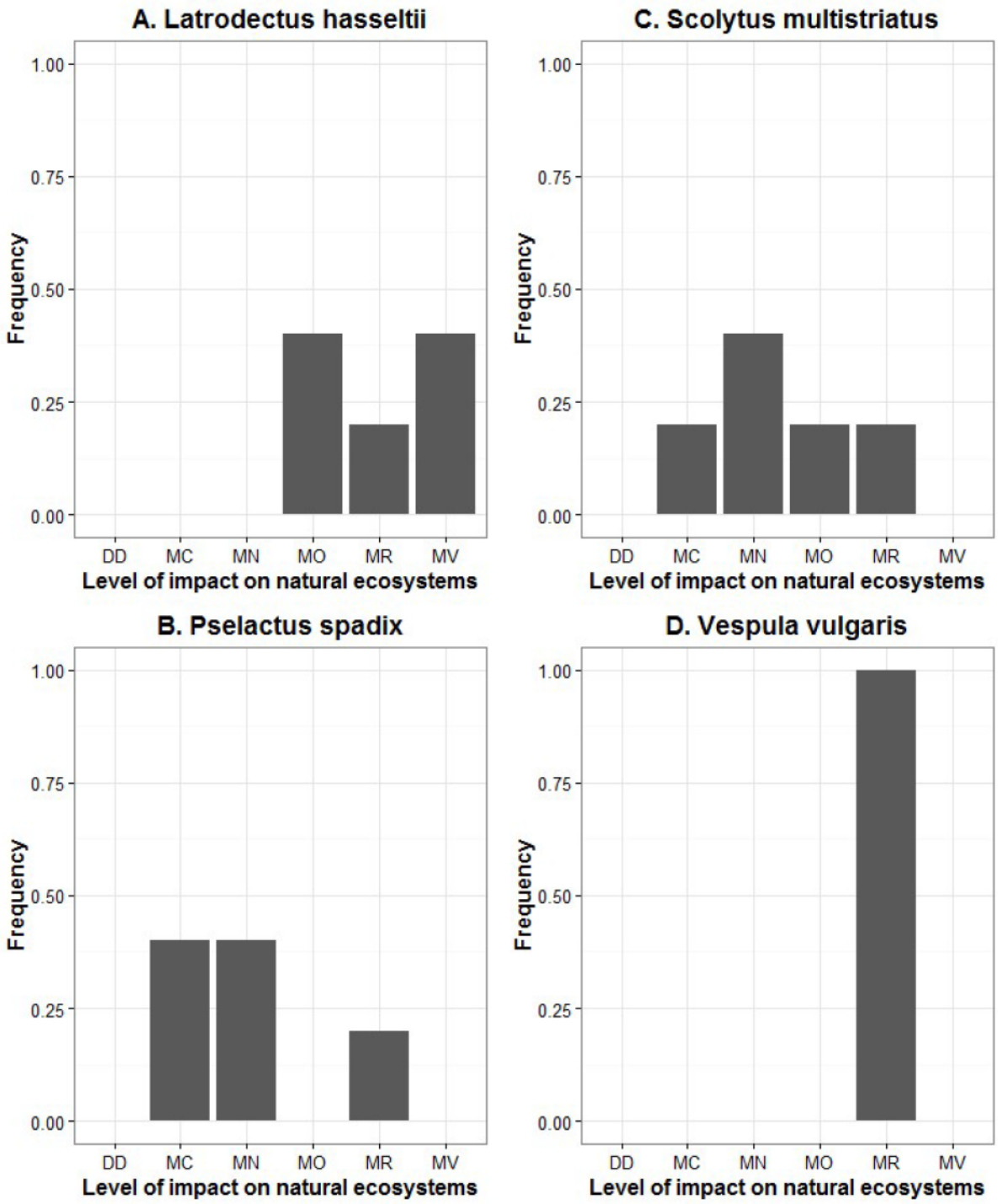


Figure 5.1 Results of overall ecological impact of the four species using Blackburn et al.'s (2014) system. The figure shows the frequency that an impact level was assigned to each species, after selecting the maximum impact level of all the mechanisms of impact.

Based on the resulting modes, experts using the Blackburn et al. (2014) system classified *L. hasseltii* as having a moderate (MO) or massive (MV) level of impact, *S. multistriatus* as having a minor (MN) level of impact, *P. spadix* as of minimal concern (MC) or minor (MN) impact, and *V. vulgaris* as having a major (MR) impact (Figure 5.1). Therefore, *L. hasseltii* and *V. vulgaris* were the species judged to have

the highest impacts on New Zealand native ecosystems, and of the four species, these two would need to be prioritized for management actions.

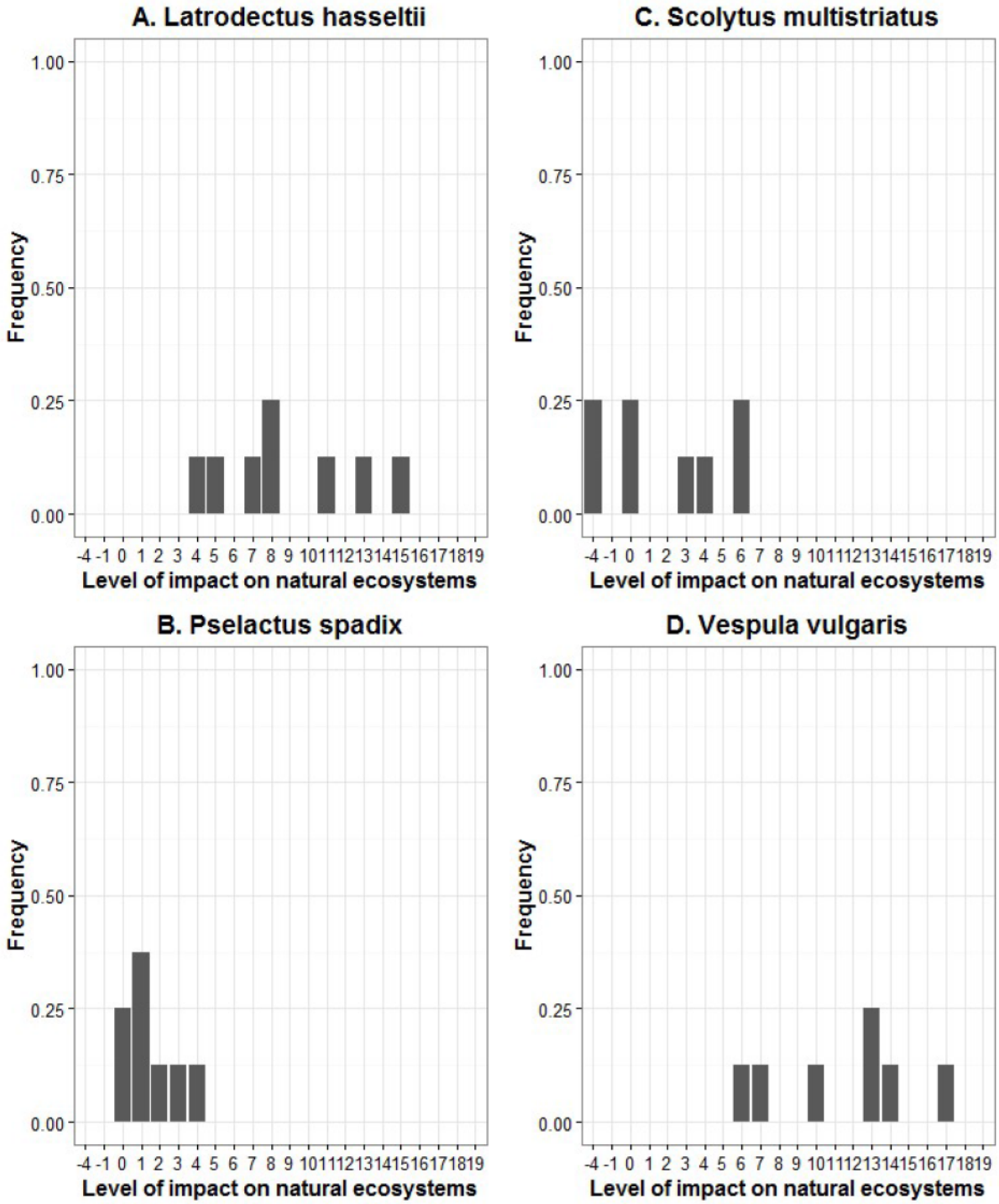


Figure 5.2 Results for overall ecological impact of the four species using Kumschick et al.'s (2012) framework. The figure shows the frequency that each level of impact was assigned to each species, after calculating the overall impact by combining positive and negative impact assessments.

Using Kumschick et al.'s (2012) system, the overall impact of the four species studied was calculated by combining positive and negative impacts (Figure 5.2). Thus, the measure of central tendency used in this case was the median. Based on the median values, *L. hasseltii* has an impact value of 8, *S. multistriatus* of 1, *P. spadix* of 1.5, and *V. vulgaris* of 13. Therefore, *V. vulgaris* is the species with highest impact on New Zealand natural ecosystems, and should be prioritized for management actions. The order in which the remaining species should be considered for management action, would be *L. hasseltii* followed by *S. multistriatus* and *P. spadix*.

5.3.2 Level of disagreement among experts

To test if the impact assessments were better than random, disagreement between experts within each classification was examined using the Spearman's rank correlation coefficient. In the first round of the expert elicitation, the median value of rank correlation coefficients between all possible pairs of participants within classifications, showed there was broad agreement between the two classification systems, this for the relative impact of each mechanism of impact for all the species (Figure 5.3). The median value of the correlation coefficient for all the possible pairs of experts was 0.463 for the Blackburn et al. (2014) framework and 0.497 for the Kumschick et al. (2012) system in the first round (Figure 5.3). With respect to the overall impact, median values of the rank correlation were 0.632 for the Blackburn et al. (2014) system and 0.600 for the Kumschick et al. (2012) system (Figure 5.4). However, there was substantial disagreement between assessors in the first round, shown in both frameworks by negative rank correlations. But at the same time, in the results of the system by Kumschick et al. (2012), some pairs of assessors using Kumschick et al.'s (2012) system agreed perfectly, with rank correlations of 1. On the other hand, negative rank correlations occurred with Blackburn et al.'s (2014) system when results of relative impact by mechanisms between pairs of participants were analysed, while no negative or perfect agreement were found in the results for the Kumschick et al. (2012) system when comparing relative impact by mechanism. Overall, there was greater disagreement between experts when assessing relative impact by mechanism with Blackburn et al.'s (2014) system. Thus, when comparing the disagreement on the overall impact of the species between pairs of participants, Kumschick et al. (2012) showed more variability, both perfect agreements plus negative rank correlations, and a greater level of disagreement compared to Blackburn et al. (2014) (Figure 5.4).

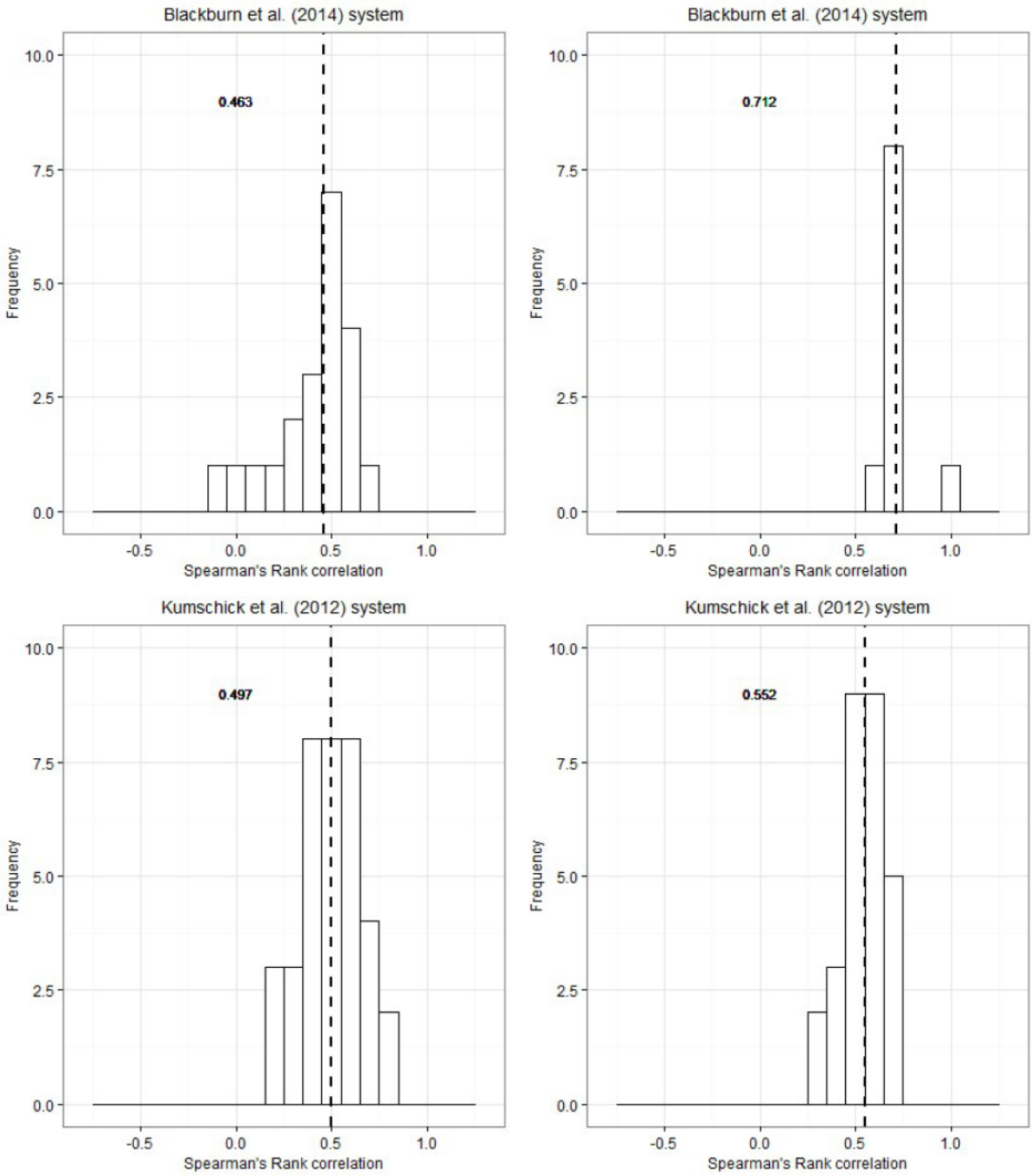


Figure 5.3 Spearman's rank correlations between the ranks of ecological mechanisms of impact of four alien species established in New Zealand, using the impact assessment methods of Kumschick et al. (2012) and Blackburn et al (2014). Values represent comparisons between pairs of participants within an impact classification system. Left figures represent the results of the first round of questionnaire responses, before discussions of the results and terms and concepts took place, while the right figures represent the results of the second round of impact evaluation and ranking after the discussions. Inside each graph the dotted line represents the mean.

Median values of the rank coefficients for the second round of elicitation were slightly higher for both systems, for both relative impact by mechanism and overall impact for each species. Moreover, the number of negative rank correlations was reduced to one instance of the overall impact of the

Kumschick et al. (2012) system (Figure 5.4). However, the number of perfect agreements between pairs of participants also decreased (Figure 5.4). For the second round, no disagreement (negative rank correlations) between pairs of participants was found for the Blackburn et al. (2014) system. As in the first round, when comparing median values of the coefficients for the two classification systems, Blackburn et al. (2014) showed a greater level of agreement between experts when assessing the level of impact by mechanism. However, when the overall impact was assessed, Kumschick et al. (2012) showed the greater level of agreement. Nevertheless, regardless of whether relative impact by mechanism or overall impact was assessed, disagreement between experts was reduced by iteration in both classification systems. However, it can not be ignored that the reduction in the number of participants between the first and the second round of the questionnaire might have influenced the variation in general agreement between the two rounds.

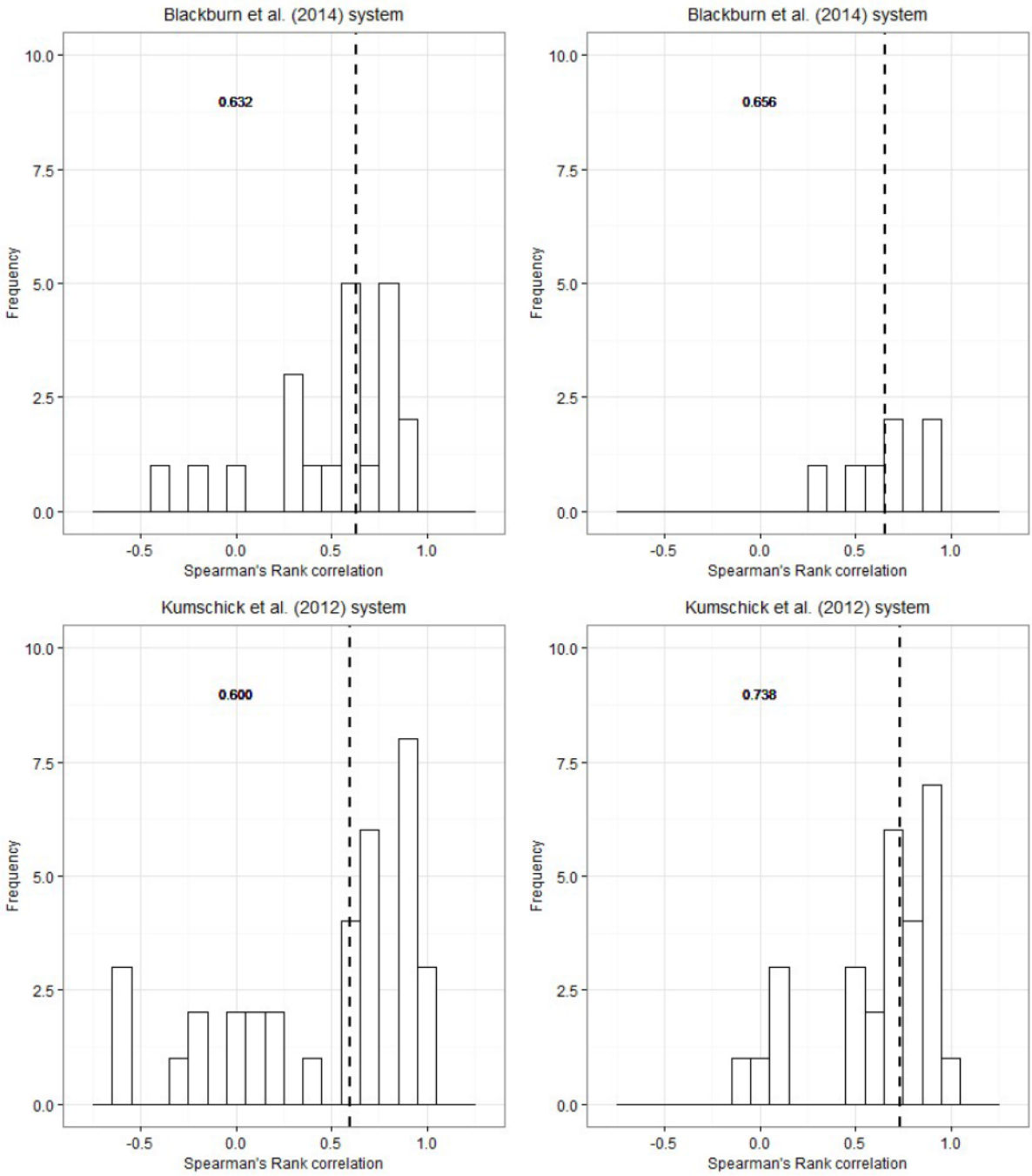


Figure 5.4 Sprearman's rank correlations between the ranks of the overall ecological impact of four alien species established in New Zealand, using the impact assessment methods of Kumschick et al. (2012) and Blackburn et al (2014). Values represent comparisons between pairs of participants within an impact classification system. Left figures represent the results of the first round of questionnaire responses, before discussions of the results and terms and concepts took place, while the right figures represent the results of the second round of impact evaluation and ranking after the discussions. Inside each graph the dotted line represents the mean.

5.4 Discussion

Results of this study show that, contrary to what I expected, the mean ranks provided by experts using two impact classification systems were not random. However, for both classification systems, there was substantial disagreement between assessors in the first round of questionnaire responses (and also perfect agreement between some participants who used Kumschick et al.'s (2012) system). Agreement between pairs of participants increased after group discussions for both classification systems. The increased median values of Spearman's rank correlation coefficients might also have been influenced by the withdrawal of some participants between the first and the second rounds, who may have lacked confidence in their expertise or were less committed to the exercise. Nevertheless, the overall result shows for both impact classification systems that structured and transparent expert elicitation protocols can improve agreement between experts while ranking impacts of IAS.

These results should be interpreted cautiously, mainly because the accuracy of the participants' responses could not be assessed. In both impact classification systems, severity categories used for impact categorization were statements about consequences that will have been influenced by the authors' personal values. Unlike facts, personal values are not assessable (Blackburn 2016). Therefore, even though there was significant agreement between participants' answers, I was unable to distinguish between accuracy and bias in the groups of experts.

When using structured expert elicitations, participants' answers are normally validated by empirical data. However, due to the qualitative nature of the severity categories used by both classification systems, the only way of assigning a level of impact as 'correct' would be to use our subjective judgement, which will be biased too. It may be argued that very severe impacts are clear-cut and less subjective, such as impacts of invasive wasps in New Zealand native beech forests. Related to this problem, authors of the GISS assume that reliability of impact ranking and the system itself relies on repeatability. Unfortunately, impact ranking by the GISS and its later adaptations is closely linked to subjective judgement (Burgman 2005; Vaes-Petignat and Nentwig 2014). The reason is that authors of the original GISS, and its subsequent applications on different taxa, validate the system by reclassifying IAS listed in the DAISIE database (Nentwig et al. 2010; Kumschick and Nentwig 2010). However, key IAS on the DAISIE database were used to state the criteria were used to create the GISS, therefore the reclassification of the species meet the authors expectations (e.g. Kumschick and Nentwig 2010). But the authors did not contemplate that species listed in the DIASIE database were previously selected by experts and therefore linked to subjective judgement.

Risk assessment is sensitive to risk perception, which is influenced by a range of psychological idiosyncrasies, subjective biases, values and conflicts of interest (Burgman et al. 2011). This includes

risks of IAS because experts typically attributed relatively more damage to invasive species in their own countries than elsewhere, and generally regard economic impacts as more severe than environmental impacts (Dahlstorm Davidson et al. 2013).

A common way to assess elicitation outcome accuracy and reliability is by testing expert knowledge. This is normally done by asking participants to give factual estimates, such as quantities, natural frequencies and probabilities (Burgman et al. 2011). These factual estimates are later contrasted with empirical data (Burgman 2016), which can be used to evaluate expert knowledge, weight opinions or exclude some opinions altogether (Burgman et al. 2011). It can also help researchers to select appropriate candidates for expert elicitation within the given context. However, even though I was aware of the assumption that expert status is a poor indicator of performance (Burgman et al. 2011), I selected experts using the profiles indicated by Blackburn et al. (2014) and Kumschick et al. (2012), which rely on expert status. Judgements of participants selected by unstructured expert selections (such the 'snowballing' selection method (Christopoulos 2009) used in this study) perform no better than random selections (Burgman 2016). Kumschick et al. (2012) also proposed an expert selection method for application only to stakeholders. Although Kumschick et al. (2012) suggested weighting stakeholder opinion to regulate their influences on impact ranks, they did not specify how to do so. Therefore, weighting decision makers will be biased by values and conflicts of interest in the same way that may happen with stakeholders and scientists, which is contrary to Kumschick et al.'s (2012) assumption.

Another important consideration for interpreting my results is that all expert estimates involve different kinds of uncertainty (Burgman 2016). Regan et al. (2002) stated that uncertainty comes in different forms, such natural (aleatory) variation, knowledge-based (epistemic) uncertainty and language-based (linguistic) uncertainty. Linguistic uncertainty has been attributed to the imprecision of our natural language, and even scientific vocabulary can be insufficiently specific, ambiguous, vague or context dependent (Burgman 2001; Regan et al. 2002). Both Kumschick et al. (2012) and Blackburn et al. (2014) acknowledged this and attempted to quantify epistemic uncertainty, but neither of them recognized the influence of linguistic uncertainty. However, because both Kumschick et al. (2012) and Blackburn et al. (2014) defined their 'severity categories' as verbal descriptions of the consequences of IAS, linguistic uncertainty is likely to be high. Both systems assumed that all the participants involved in the impact ranking had the same interpretation of defining terms and concepts regarding IAS impact ranking, which is unlikely (Burgman 2005). Thus, increased agreement between participants will be partly attributable to a greater shared understanding of the context and definitions of the terms regarding the risk assessment (Burgman 2005). But although some disagreements might have been resolved given further discussion and re-definition, increased consensus may not always be the result

of reduced linguistic uncertainty, but rather arise from greater agreement about vague definitions (Burgman 2001). Linguistic uncertainty was specifically assessed in both systems (see Appendix D.2), and agreement between the participants' opinions on the clarity of the systems generally improved after discussion. Participants agreed on the clarity of Blackburn et al.'s (2014) 'severity categories', although they acknowledged indeterminacy in some of the theoretical terms used in the questions. Indeterminacy refers to the fact that future usage of theoretical terms is not completely fixed by past usage, so there is potential ambiguity due to the open texture of language (Regan et al. 2002). Participants in this study seemed to reach a consensus on when to choose between *Data Deficient* and *Minimal Concern* impact values in the Blackburn et al. (2014) system. In contrast, participants who used Kumschick et al.'s (2012) system went from substantial disagreement about linguistic uncertainty to random assortments of levels of linguistic uncertainty. Contradictory results between Kumschick et al. (2012) and Blackburn et al. (2014) might be related to linguistic uncertainty, but also to the questions regarding linguistic uncertainty were formulated. Although participants using both systems were provided with the same questions and definitions of terms (See Appendix D.3), it is likely there was still linguistic ambiguity.

Another factor that is likely to have influenced the increased agreement between participants is the aggregation technique chosen. The Delphi technique was created to facilitate group discussion and decision making among acknowledged experts, but with the final aim of reaching a consensus (Goodman 1987; Burgman 2005). This has been criticized for limiting interactions between experts and dealing inadequately with uncertainties (Burgman 2005). It encourages uniformity and discourages dissent (Burgman 2005), and its mechanisms for resolving differences tend to fuel expert overconfidence because when experts adjust their own opinions they tend to do it in the direction of the supposed 'leading' experts, rather than in the direction of the strongest arguments (Burgman 2005; Aspinall 2010). Thus, the Delphi technique might not adequately deal with some cognitive frailties that compromise the accuracy and reliability of expert opinions (Burgman 2005). Other aggregation techniques weight the opinion of each expert on the basis of their knowledge and ability to judge relevant uncertainties, such as the Cooke method (Cooke et al. 2008), which might be more effective (Aspinall 2010).

5.4.1 Recommentations and future directions: is conservation biology pointing the way?

The efforts of the GISS authors are commendable. Much thought has gone into the developing, testing and implementating a generic tool to classify the impacts of diverse IAS taxa in different environments, particularly when considering local effects that are difficult to assess (Parker et al. 1999; Goodell et al.

2000). However, a quantitative system is likely to help obtaining an accurate and reliable impact ranking systems as it has been shown in the literature (Burgman 2001; 2005; 2011; 2016).

As Sandvik et al. (2013) pointed out, quantitative risk assessments have several advantages over qualitative ones. The most obvious is that they are free of linguistic uncertainty (Burgman 2001). Also, they are less influenced by subjective judgements (Burgman 2001; McCarthy et al. 2004), have greater transparency and repeatability (Mrosovsky 1997), and treat uncertainty in a standardised way (Stone et al. 1994). Moreover, quantitative impact assessments allow expert knowledge to be evaluated and weighted, and some experts' opinions to be excluded (Burgman et al. 2011). Thus, structured expert elicitation could be conducted with more reliable outcomes that may allow better prioritization of management actions.

Conservation biology has been using structured expert elicitation more successfully and for longer than invasion biology to, for example, estimate risks of extinction. McBride et al. (2012) successfully combined the IUCN Red List criteria with a structured elicitation of expert judgement for threatened species assessment. The authors use terms specifically defined under the IUCN criteria to create 16 quantitative parameters and up to 33 categorical parameters, and those parameters were elicited from experts for each taxon. For the quantitative parameters, experts were requested to estimate quantities and percentages by providing a minimum and maximum value, their best estimate (or the most likely value) and a confidence interval. Moreover, for the categorical parameters experts were asked to identify whether a statement is true or false, and to provide a certainty estimate of their answer, in the range of 50-100%.

The only IAS impact assessment tool that seems to follow a similar structure, and integrates the three dimensions of impact proposed by Parker et al. (1999), is the generic impact assessment of IAS created by Sandvik et al. (2013) for Norway. This semi-quantitative tool combines quantitative and qualitative approaches on two axes resulting in a final impact category, as explained in the results section of this chapter. However, to my knowledge, the approach by Sandvik et al. (2013) has not been as widely used as the GISS. As authors of some impact assessment tools admit, there will never be a perfect classification, but I believe that more research is needed on this interesting and challenging topic. I think a quantitative impact ranking system that integrates all dimensions of environmental effects with economic and social effects would help to manage IAS more effectively and with more accurate information about their impacts.

Chapter 6

General discussion

The main aim of this thesis was to increase knowledge that will help to improve risk assessment of the potential establishment and impact of non-native arthropod species which represent a threat to ecosystems. The actual research was built on a preliminary study by Phillips et al. (2008), which indicated that several factors could be key to assessing the risks of establishment, spread and impact of non-indigenous invertebrates in novel natural ecosystems. Those factors were biogeography, climate, host availability at the invaded site and level of host specificity. Additionally, further research had suggested that measures of plant community similarity and more advanced measures of host relatedness in the invaded range could also be important (Gilbert et al. 2012; Bacon et al. 2014; Bebber et al. 2014). Thus the specific thesis objectives to achieve the overall aim were firstly to revise the taxon-specific databases developed as part of the Phillips et al. (2008) review, by adding new published records of species of non-native beetles and spiders established in New Zealand and North America, and to classify them according to their known impact on natural ecosystems in the two geographic regions (Chapter 2). Secondly was to compare the level of impact on North America and New Zealand natural ecosystems of non-native beetles and spiders to determine the potential differences between continental and oceanic island ecosystems, and assess the influence of host specificity and biogeographic affinities (Chapter 2). Thirdly was to determine the importance of climate, plant similarity and plant diversity in the invasive range for risk assessment of the potential impact of non-native invertebrates (Chapter 3). Fourthly, to determine if phylogenetic affinities analysis, can give useful predictions to evaluate the relative impacts of non-native species on individual hosts and ecological systems was considered (Chapter 4). Finally, a review of the different impact classification frameworks available was undertaken and the sensitivity of impact assessments using well-established ecological impact classifications to help identify the sources of uncertainty related to such systems was tested (Chapter 5).

6.1 Differences between non-native beetle and spider species within selected ecosystems

A tool that has proven very useful for determination of the general patterns characterising invasive species and invaded habitats are non-native species inventories (Kenis et al., 2007). Thus, the identification and listing of non-native species successfully established in different regions of the world is considered an essential tool for management of biological invasions (Ricciardi et al., 2000; Kolar and Lodge, 2001; McGeoch et al., 2010). However, information about the non-native species, especially invertebrate species, already present in natural ecosystems, is generally poor compared to that for

modified ecosystems, but is essential for risk analysis. When a non-native species inventory for an ecosystem is available it can help to identify important characteristics of the species and of the novel ecosystems that may influence the invasion process. For example, it has been stated that because novel environments present several filters that non-native species must overcome, successful invaders may not be a random selection of species (Karatayev et al. 2009; Wilson et al. 2009). As a result, communities of non-native species in a geographic region may be dominated by species from particular geographic origins (e.g. Niemelä and Mattson, 1996; Langor et al. 2009). In addition, the importance of biogeographic relationships between geographic regions might depend on the taxa studied and their level of host specialisation. Non-native species inventories can also help identify more sensitive ecosystems. For example, it is frequently argued that continental communities are more resistant to invasion than island communities (Mooney and Cleland 2001; Martínez et al. 2007; Corlett 2010) mainly due to differences in species diversity (Herben 2005). Therefore, this research began with a revision of the existing taxon-specific databases provided by Phillips et al. (2008) that recorded established species of phytophagous beetles and spiders in New Zealand and North America, and information on their effects on natural ecosystems and other native species. New records of established species were added, and information on their effects on natural ecosystems and native species was updated. The new version of the database allowed species' impacts to be reclassified to analyse and compare the effects of both taxa on native biota in both target regions.

This comparison indicated that North American natural ecosystems appear more vulnerable to phytophagous insect invasion than those in New Zealand, while New Zealand natural ecosystems are comperatively more sensitive to invertebrate generalist predators as represented by spiders. In New Zealand, occurrences of non-native beetles feeding on native species are rare, with their impacts minor and normally caused by the polyphagous species. Differences in the level of impact of non-native beetles and spiders between the selected regions highlighted an ecological characteristic that seems to be an advantage for non-native invertebrates in New Zealand, and that is their degree of polyphagy or host generality. Thus, island communities, at least in New Zealand, are generally more invasible by host-generalist invertebrates than continental ecosystems, such as North America. Previous studies on New Zealand non-native phytophagous species have indicated that polyphagy may strongly influence not just establishment success but also the impact on native ecosystems (e.g. Peacock and Worner 2008; Martin and Paynter 2014). For example, Martin and Paynter (2014), on a study of non-native Acari and Insecta herbivores in New Zealand recorded as attacking indigenous plants, stated that the polyphagy is a common characteristic of many invertebrate arthropods recorded on New Zealand indigenous plants. Actually, Roderick and Navajas, (2015), in their study outlining the main mechanisms and pathways by which terrestrial arthropods invade new habitats, highlighted that successful non-native arthropods share similar biological features, such as host generality or polyphagy. It has been hypothesized that species with low host specificity might have a higher number

of hosts or prey available in the invaded area than species with high specificity. That in turn is likely to reduce the time required to search for new hosts or prey and additionally increase the geographic range of the invader (Peacock and Worner, 2008; Barret and Heil, 2012). Therefore, the influence of polyphagy on establishment success, but also on the impact of non-native arthropod herbivores on native ecosystems, should be further investigated. Unfortunately, such an investigation was an initial objective of this research but became out of scope due to the time frame available.

With respect to biogeographic origins, approximately half the non-native phytophagous beetles and spiders causing impacts in New Zealand native ecosystems are Australasian, and a quarter are Neotropical with a native range in either South or Central America. While in North America, most of the non-native species studied are Palearctic, but host specificity of the non-native beetles is much more variable. Despite the absence of a significant relationship between impact and species-origin in this study, with the exception of non-native spiders in New Zealand, other studies have demonstrated that biogeographic origin of non-native species can be an important factor for species establishment. For example, Ward and Edney-Browne (2015) found that biogeographic origin is an important filter when comparing intentional with unintentionally introduced non-native Hymenoptera species in New Zealand. Thus, patterns on the biogeographic origin of the species in both groups were significantly different (Ward and Edney-Browne 2015). Moreover, Martin and Paynter (2014) demonstrated that adventive herbivores feeding on New Zealand indigenous plants, which would be considered at least as a minor impact, varied significantly according to arthropod order and family and their degree of polyphagy. Therefore, the apparent agreement between these results and the IRA hypothesis statements is probably due to the ecological characteristics of the specific taxonomic groups studied.

A potential limitation of the research in this chapter, is how the data has been analysed. When structuring the data in contingency tables for the analysis of the relation between the level of impact of the species and their geographic origin, the data became unequally distributed among the cells and some cell counts were equal to zero. This was the reason why the Fisher's exact test was chosen over of the chi-squared test, despite that the sample size was quite large. However, neither of these methods allow anything other than null hypothesis significance testing (NHST). NHST has been repeatedly criticised by many distinguished scholars, and identified as a major source of many of the problems with research integrity, and branded as retarding research progress (Cumming 2014). The main problem with NHST is that forces researchers to adopt a dichotomous point of view, and formulate aims and conclusions accordingly, which gives an apparent illusion of certainty (Kirk 2003 cited by Cumming 2014). In hindsight, effect sizes, estimation and accumulation of evidence may give an accurate quantification of uncertainty that provides a much better way to analyse results (Cumming 2014). Therefore, to confirm if the geographic origin of the non-native species studied really does not influence their level of impact on natural ecosystems, other analytical tools that allow, for example the calculation of confidence intervals, should be used, such as generalized linear models (GLMs).

6.2 Floristic and climatic similarity to determine impact of non- native phytophagous species

Non-native species risk assessment to prevent their establishment in new environments, involves the identification of abiotic and biotic factors that allow the species to form persistent populations (Vanhanen, 2009). Some of those factors have been widely studied and used for risk assessment, while others have been proposed recently or are investigated in novel ways in this thesis.

One of the most common environmental factors used to predict the potential distribution of non'native species is climatic similarity. However, several authors have recently argued that such models rarely acknowledge that species evolve and adapt to new conditions, and that the occurrence data used to parameterise their models are likely to be a small subset of the abiotic conditions conductive to population growth (Sax et al. 2007; Bebber 2015). Thus, it is unclear how precise the predictions based on a species current known distribution can be (Sax et al. 2007). However, it has been stated that non-native pests, given that the climate is suitable, can establish wherever their hosts occur (Bebber 2015), and that host availability is crucial for successful colonisations of phytophagous invertebrates (Niemelä and Mattson, 1996; Bacon et al., 2014). Clearly plant community characteristics in the invaded region could be important. Therefore, the influence of climatic and floristic similarity between regions, as well as floristic diversity within each region, on non-native beetle occurrences was investigated and compared in this thesis. The results demonstrated that floristic similarity between regions in combination with floristic diversity within a region may better predict the presence of non-native beetle species than climatic similarity alone. However, including floristic and climate variables in the same model gave a better fit to non-native beetle presence than models that included either variable separately, as has been found in other studies (e.g. Bebber et al. 2014; Sutherst, 2014).

Davies et al. (2005) and Fridley et al. (2007) have demonstrated a positive relationship between plant species diversity or richness and successful establishment of non-native phytophagous species. The importance of floristic diversity, estimated in this study using Faith's phylogenetic diversity (Faith 1992; Kembel et al 2010), was significant in the New Zealand individual species models predicting their establishment. In fact, Faith's phylogenetic diversity was the most important variable, explaining the highest percentage of deviance of non-native beetle species presence. However, this variable should have been analysed separately from similarity measures for a better interpretation of the results. Unlike climatic and floristic similarity, floristic diversity was not compared between regions.

With regard to floristic similarity quantified in this study using the Jaccard similarity index (Jaccard 1912), this variable was demonstrated to be an important factor that could improve geographic risk assessments of the potential for establishment of phytophagous non-native invertebrate organisms.

This would be important especially for making rapid initial assessments of species establishments when little biological information is available (Kriticos 2012). This research suggests that plant community similarity should be routinely used along with the simple match climates index obtained from the Regional Match Climates module in CLIMEX (C. Phillips and J. Berry, personal communication), to make improved assessments. Despite the results indicating the value of including floristic similarity within the geographic risk assessment, my data only allowed the analysis of plant similarity at a coarse resolution, which comprared one measure of plant similarity per region. On the other hand, the Regional Match Climates module in CLIMEX, allows the identification of the threat of pest establishment at a finer resolution (Sutherst and Maywald, 1985; Sutherst et al. 2007; Kriticos, 2012). Future research could focus on gathering quality data to further analyse the influence of regional plant and climate similarity on non-native pest species presence, to identify particular threat regions globally.

6.3 Host plant phylogenetic signal to determine the potential impact of non-native phytophagous species

The final factor assessed in this thesis was whether plant phylogenetic signal could predict potential non-native phytophagous insect establishments in New Zealand natural ecosystems (Chapter 4). Additionally, it was investigated whether such a measure could also be used to predict which native plants might be more likely to be threatened by species of non-native beetles recorded in the GPDD database, as well as which of these species were more likely to feed on New Zealand native plants. Phylogenetic signal is defined as 'the tendency of related species to resemble each other more than those drawn at random from the same phylogenetic tree' (Blomerg and Garland 2002). This concept has been demonstrated to be a useful tool for phytosanitary risk analysis by Gilbert et al. (2012), who measured the strength of the phylogenetic signal in the global host range of nine major groups of pests and pathogens. Moreover, Gilbert et al. (2015) also linked phylogenetic signal to the severity of impact of herbivore-host interactions. However, as herbivore-host surveys used for this kind of analysis, normally have a strong bias toward species of economic interest, as a consequence is a limited coverage of native plants (Pyšek et al. 2008; Gilbert et al. 2012). Furthermore, often only plant susceptibility is recorded, and records of plant resistance are rarely included in pest-host databases. Such bias can lead to many false negatives (Gilbert and Webb, 2007; Gilbert et al. 2012). In this study however, it was assumed that the survey bias in the NZNH database was smaller than in the GPDD database, because NZNH authors focussed on identifying non-native invertebrate herbivores feeding on New Zealand native plants (Martin and Payner 2014).

In agreement with the literature discussed here, host-ranges of non-native phytophagous species established in New Zealand appear phylogenetically constrained, thus closely related plant species are

more likely to share non-native phytophagous species. Despite that general result, when analysing the different insect orders individually, some discrepancies were found between the host-ranges of the species in this analysis and results from other studies. For example, the study by Martin and Payner (2014), using a previous version of the NZNH database, identified Hemiptera species as one of the greatest risks for New Zealand native plants because of the high number of records and their broad host range. In the current study, based on the analysis of the relation between pest presence, the number of known hosts and the phylogenetic distance between hosts, Hemiptera species were indicated as likely to feed on a narrow range of closely related plant species. In contrast, Thysanoptera and Diptera show a wider range of potential hosts and seem to feed on less closely related species, but these are the groups with fewer records in the NZNH database. As Gilbert et al. (2012) caution, the probabilities estimated by the phylogenetic analysis can represent an extrapolation beyond the range of data used to parameterise the models, such that differences between groups need to be carefully interpreted. Thus, results from this analysis are likely to be biased by the number of records and species in each taxonomic group as extrapolation is more likely higher with smaller sample sizes.

Despite that discrepancies between the Martin and Payner (2014) findings and the results presented in Chapter 4 might be explained by potential extrapolation and differences between empirical range tests, one would expect a clear relationship between host specificity and host phylogenetic distance. Therefore, the relationship between those two variables needs to be further investigated. One way to investigate the relation between host specificity and host phylogenetic distance, would be to compare indices of host phylogenetic diversity with traditional classifications of host specificity, which are generally explained by plant evolutionary relatedness (Weiblen et al. 2006). Traditionally, host specificity of species (e.g. monophagous, oligophagous and polyphagous) is usually based on a species entire geographical range, or in other words, on all its known hosts. Also, because host specificity can show a spatial turn over, indices of host phylogenetic diversity at different scales vary from traditional classifications (Lewinson et al. 2005; Poulin et al. 2011) and could explain the discrepancies between the literature and Chapter 4 results. Regarding potential phylogenetic indices for future analysis, indices such as the nearest taxon index (NTI) and the net relatedness index (NRI) could be used (Webb 2000; Webb et al. 2002). For example, Weiblen et al. (2006), in a study analysing the phylogenetic dispersion of host use in a tropical insect herbivore community, used these indices to quantify the extent of phylogenetic clustering in particular herbivore associations. Other indices such as the Faith's phylogenetic diversity (PD) and the mean phylogenetic distance (MP) could also be used if information on the plant community of where the pest species occur, are available (Faith 1992; Webb et al. 2002). These last two indices have been used, for example, by Lind et al. (2015), to examine the influence of evolutionary relatedness on arthropod traits, feeding associations and co-occurrences in community ecology.

Despite these caveats, my results seem to support the use of a phylogenetic signal as a reasonable approach to the prediction of the likelihood of coleopteran pests feeding on New Zealand native plants when empirical data is limited. The results indicate which native New Zealand plant genera would be more likely to be susceptible to Coleoptera species recorded in the GPDD database. According to the results, six species are already present in New Zealand, from the 96 species listed as potential threats to New Zealand native plants, and that were ranked depending on the number of known hosts and the probability to feed on a closely related plant species. Of those six species, one is native (*Costelytra zelandica*) and five are non-native species already established (*Heteronychus arator*, *Epilachna (Henosepilachna) vigintioctopunctata*, *Naupactus leucoloma*, *Amasa truncate*, and *Phoracantha semipunctata*). Ten other genera have another species from the same genus already established in New Zealand. Regarding New Zealand native plants, 54 genera are likely to be suitable hosts for the non-native species of beetles of the GPDD database. Plant genera that have the highest probability of sharing a common pest species are those in which a pest species has already been recorded. Of the 13 genera, *Solanum* seems to be at particularly high risk. In fact, four of the six species discussed above feed on New Zealand native *Solanum* species.

Results for both, potential New Zealand native hosts and the non-native beetles that threaten them, suggest the utility of host phylogenetic signal as a tool for phytosanitary risk analysis. However, because of the assumptions and conjectures of extrapolation and potential differences with empirical host range tests highlighted by Gilbert et al. (2012), I recommend to use this tool as a filter for more detailed risk assessments. Thus, plant phylogenetic analysis could be useful to regulatory authorities, such as the Ministry for Primary Industries (MPI) in New Zealand, and others around the world, to rapidly evaluate the host range of a newly detected invader and decide on appropriate management actions. Host phylogenetic affinities analysis can help to prioritize empirical tests and individual herbivore risk assessments on high risk-ranked herbivore species, and therefore be used as another tool for risk assessment protocols. Similar to what it has been done for forest plantations by Castagneyrol et al. (2014), phylogenetic distance can help identify vulnerable plant communities to help prevent and manage potential non-native phytophagous establishments.

6.4 Non-native species' impact classification tools and their assessment

The analysis and comparison of non-native species impacts in Chapter 2 raised other questions besides those derived from the interpretation of the results. Clearly, impact assessment is an important part of managing invasive species and current methods needed to be reviewed. The literature review of the different impact assessment tools available to risk assessors showed that there are multiple options available, however most of them are of a qualitative nature which can lead to inconsistencies between

assessors (Kumschick and Richardson 2013). Furthermore, risk assessment has been demonstrated to be sensitive to risk perception, which is highly influenced by a range of psychological idiosyncrasies, subjective biases, values and conflicts of interest (Burgman et al. 2011). Such discussion raises the question about how the use of different impact classifications might affect non-native species risk ranking.

A number of impact assessment tools are available in the literature. However, special attention was given to the Generic Impact Scoring System (GISS) (Nentwig et al. 2010), which to my knowledge is the method that has been most well developed and widely used (Nentwig et al. 2016). The GISS represents the attempt of a number of scientists to create a standardized tool to quantify and compare impacts among taxonomic groups and geographic regions (Nentwig et al. 2010; Kumschick and Nentwig 2010; Nentwig et al. 2016). Two specific adaptations of the GISS, Blackburn et al. (2014) and Kumschick et al. (2012), were used in this thesis to test if the resulting impact assessments, as a result of their use, were better than random. To overcome the subjective biases and uncertainties that strongly influence risk ranking, expert knowledge elicitation and encoding methodologies are commonly used. Therefore, a combination of the Delphi technique and the nominal group technique (NGT) was used following the McBride et al. (2012) and Mukherjee et al. (2015) elicitation protocol. Contrary to what was expected, the agreement between experts using the two GISS adaptations, calculated using the Spearman's rank correlation coefficient (Burgman 2001), was far from random assortments of ranks. While there was a considerable disagreement, initially indicated by negative correlation coefficients, conformity increased after discussion among experts. But, as suggested in Chapter 5, these results need to be interpreted with care. One of the reasons is because of potential linguistic uncertainty linked to statements used in both adaptations to describe the severity categories. Research by Burgman (2001) and Burgman (2005) suggests that the potential improvement in the level of agreement between participants can be attributable to an improvement in the shared understanding of the context and definitions used. Another reason is that the nature of the impact classification systems did not allow the assessment of the accuracy of the participants because, unlike facts, values are not assessable (Burgman 2016). Therefore, even though there was apparent agreement between participants' answers, I was unable to distinguish between accuracy and bias for the whole group of experts.

The application of a structured expert elicitation process, such as the one used in this research, allows researchers to measure the repeatability of the results, measured as agreement between the answers of the experts. However, the inability to measure the accuracy or reliability of the outcomes in this study can render the overall and relative magnitudes of impact resulting from the assessment wrong (Burgman 2001). For that reason, future efforts should be directed to develop a generic quantitative impact assessment system. It is widely known that quantitative risk assessments have a number of

advantages over qualitative ones (Sandvik et al. 2013). Quantitative assessments are free of linguistic uncertainty (Burgman 2001), have a reduced influence of subjective judgements (Burgman 2001; McCarthy et al. 2004), an increased transparency and repeatability (Morsovsky 1997), and a standardised treatment of uncertainty (Stone et al. 1994).

Quantitative assessments also allow the evaluation of expert knowledge, weighting their opinions or excluding some opinions altogether (Burgman et al. 2011). Moreover, in the particular case of assessing the impact of non-native species, a quantitative approach would allow the integration of the three dimensions proposed by Parker et al. (1999) to assess the total ecological effect. In fact this has already been attempted in Norway by Sandvik et al. (2013), who developed a semi-quantitative tool that combines quantitative and qualitative approaches to attribute to the non-native species a final impact category.

However, it cannot be ignored that the integrative quantitative model proposed will be complex to develop and more importantly, to apply. While quantitative approaches might be more precise, qualitative approaches seem easy to understand, even though interpretation might be different by different users and that the normative opinion of the authors of any qualitative framework may be included (IPPC 2005; Weiss 2006). As a consequence, interesting attempts have been made to develop a quantitative generic framework to assess non-native species impacts, but have not succeeded in their aim of being widely used, such as the approach proposed by Sandvik et al. (2013). It seems then that effort should be directed to develop a user friendly quantitative framework that can be applied through a structured expert elicitation process, which encourages the participation of researchers, practitioners, stakeholders and decision makers. It is suggested that such integration would ultimately allow more effective management strategies against non-native species.

6.5 Conclusions and major findings

This research has contributed to increased knowledge and awareness of the range of factors that can determine or influence non-native species establishment success and subsequent impact. New ecological filters or variables of influence have been identified, such as floristic similarity and diversity within regions, which can be added to climate similarity to assess impact. Additionally, host phylogenetic distance was also found to be a useful variable. By recognising potential shortcomings in the research, as well as identifying future directions, I believe this research will improve assessment of the potential establishment and impact of non-native arthropod species in natural ecosystems. Additionally, I expect that this new knowledge will improve pest and disease risk assessments for productive ecosystems in general. More specifically however, this research will help policy makers and

risk managers to better prioritize their actions and efforts against species that can represent a serious threat for native ecosystems.

The major findings on this research have been that:

- North American natural ecosystems seem to be more vulnerable to phytophagous insect invasions than New Zealand, while New Zealand natural ecosystems are more sensitive to invertebrate generalist predators, such as spiders.

- There was no clear relationship between biogeographic origin of the non-native invasive species and its potential to establish and cause impact in either ecosystem studied.

- New Zealand, representing an oceanic island ecosystem, appears to be more invasible by host-generalist invertebrates than a continental ecosystem, such as North America.

- Plant floristic similarity between regions in combination with floristic diversity within a region better predict the presence of non-native beetle species than climate similarity alone. However, including floristic and climate variables in the same model better predicted non-native beetle presence than models that included the variables separately.

- The host-range of non-native phytophagous species established in New Zealand are phylogenetically constrained, however the phytosanitary risk determined by the phylogenetic signal of plant hosts varies among classes of herbivore taxa and among orders of phytophagous insects.

- Host phylogenetic signal can allow risk assessors to identify potential threats to flora present in a target region and to prioritize phytophagous species for future empirical tests.

- Current impact assessment frameworks available are of a qualitative nature which can lead to inconsistencies between assessors.

- A structured expert elicitation process would increase the agreement between experts, even when qualitative frameworks are used, that rank the impacts through statements about important consequences, such as severity categories or values determined by the authors.

- Most of the published qualitative impact assessments are based on values, and do not allow accuracy and reliability of the experts' opinions to be tested.

Appendix A

Impacts of alien beetles and spiders in natural ecosystems of continents and oceanic islands

A.1 Tables of non-native beetles and spiders established in the natural ecosystems of North America and New Zealand

Table A.1.1 Non-native beetles established in North American natural ecosystems.

Genus	Species	Species author	Impact level	Details	References
Anthonomus	*grandis*	Boheman, 1843	minor	Larvae mostly develop in reproductive structures or in galls, it also feeds primarily on several genera within the tribe Gossypieae of the family Malvaceae, which includes North American natives.	invasive.org 2015; Arnett et al., 2002; http://www.cabi.org/isc/datasheet/5735; Dickens, 1984
Anthonomus	*pomorum*	Linnaeus	minor	Species are associated with various families of plants including Asteraceae, Caprifoliaceae, Cistaceae, Cupressaceae, Euphorbiaceae, Fabaceae, Juglandaceae, Krameriaceae, Malpighiaceaem, Malvaceae, Myrtaceae, Rosaceae, Rutaceae, Salicaceae, Solanaceae, and Vitaceae; larvae mostly develop in reproductive structures or in galls	O'Brien and Wibmer, 1982; http://www.cropscience.bayer.com/en/Crop-Compendium/Pests-Diseases-Weeds/Pests/Anthonomus-pomorum.aspx ; Arnet et al., 2002
Apion	*curtirostre*	Germar	omajor	This weevil develops in various species of Rumex and may be of use in the suppression of the weed curly dock *(R. crispus*), though equally it may destroy indigenous species of Rumex that are of importance in wildlife management.	O'Brien and Wibmer, 1982; CABI; Whiterhead, 1980
Archarius	*salicivorus*	Paykull	minor	Introduced in Canada (Quebec). Associated with *Salix* (willow) and *Curculio villosus,* in *Biorhiza pallida* apple galls on oak (*Quercus*sp.), development of the larvae in the bile of sawflies. Also known as *Curculio salicivorus*.	Langor et al. 2009: Ghahari et al. 2010
Baris	*lepidii*	Germar	minor	Attacks horseradish (*Armoracia rusticana*) by feeding on the roots and oviposition in them. Reported in crucifer. It was reported in horseradish in Illinois, and weevils and eggs found in a commercial field of turnips.	O'Brien and Wibmer, 1982; CABI 2015; Bouseman et al. 1978

Barynotus	*obscurus*	Fabricius, 1775	minor	Is known in Canada from the Atlantic Provinces and from British Columbia. Adults are reported to have attacked young tobacco plants in Prince Edward Island and injured strawberries in Nova Scotia. The species has also been reported to damage the crown and leaf stems of small fruits in Nova Scotia. Is a polyphagous on numerous species of herbaceous plants, such as Trifolium, Primula, Medicago, Vicia, Rosa, etc.	O'Brien and Wibmer, 1982; Brigth et al., (Weevils of Candada and Alaska: Coleoptera, curculionidae, entiminae); Arnett et al., 2002
Barypeithes	*pellucidus*	Boheman 1834	omajor	*Polydrusus sericeus, Phyllobious oblongus*, and *Sciaphilus asperatus, Barypeithes pellucidus, Calomyceterus setarius, Otiorhynchus ovatus, Pachyrhinus elegans, Strophosoma melanogrammum,* and *Trachyphloeus aristatus* composed the >80% of the total individual weevils collected in North American northern hardwood forests. These last six species are less abundant although they may be contributing at the displacement of native species of weevils in native ecosystems.	Pinski et al., 2005
Betulapion	*simile*	Kirby 1811	minor	Generally distributed in North America. Adventive on *Betula papyrifera* Marsh. (Paper brish; Salicaceae); larvae develop in flowers.	Arnett et al., 2002
Callirhopalus	*bifasciatus*		minor	The twobanded Japanese weevil attacks a broad range of hosts, including cherry laurel, broad-leaved evergreens, pyracantha, privet, barberry, euonymus, forsythia, lilac, strawberry, mountain laurel, great rhododendron, multiflora rose, Allegheny blackberry, American bittersweet, flowering dogwood, gray dogwood, bittersweet nightshade. The Florida specimens were collected sweeping in a soybean field. Wheeler and Boyd (2005) called it "an important pest of landscape plantings in the northeastern and Midwestern" states, but noted that it has "received scant attention in the Southeast."	O' Brien and Wibmer, 1982; Aukema et al. 2010; Wheeler and Boyd, 2005; http://www.freshfromflorida.com/Divisions-Offices/Plant-Industry/Plant-Industry-Publications/Pest-Alerts/Pest-Alerts-The-Twobanded-Japanese-Weevil
Calomycterus	*setarius*	Roelofs 1873	omajor	*Polydrusus sericeus, Phyllobious oblongus*, and *Sciaphilus asperatus, Barypeithes pellucidus, Calomyceterus setarius, Otiorhynchus ovatus, Pachyrhinus elegans, Strophosoma melanogrammum*, and *Trachyphloeus aristatus* composed the >80% of the total individual weevils collected in North American northern hardwood forests. These last six species are less abundant although they may be	Pinski et al., 2005

				contributing at the displacement of native species of weevils in native ecosystems.	
Cionus	*scrophulariae*	Linnaeus	minor	This adventive Palaearctic species, which is associated with *Scrophularia* and *Verbascum* (Scrophulariaceae), is known to be established in New York.	Douglas et al. 2013
Cylas	*formicarius*	Fabricius, 1798	minor	Exotic Insects which have become major pests in the US agriculture. Hosts: *Ipomoea batatas* and forty nine other members of the Cunvolvulaceae (oligophagous) and also feeding on members of the Acanthaceae, Cruciferae, Euphorbiaceae and Umbelliferae (polyphagous).	http://www.cabi.org/isc/datasheet/17408
Cryptorhynchus	*lapathi*	L.	omajor	It is found in southern North American forest and grassland ecosystems. Both species are polyphagous and feed on various family plants. This species feeds on Salix, Populus, Alnus, and Betula. It has been reported causing severe damage and mortality to native willow stands in British Columbia and Ontario. This species also bores alders, and is a pest of hybrid poplars, such as *Populus x jackii* (blam-of-Gilead).	Kirkland and Mass, 1899; Coyle et al., 2005; Hannon et al., 2008
Cyphocleonus	*achates*	Fahraeus 1842	minor	Found in Colorado, Wyoming, Montana, Oregon and British Columbia. This species was introduced as a biological control agent for *Centaurea maculosa* Lam. (spotted knapweed) and *C. diffusa* Lam. (diffuse knapweed) (Asteraceae). It has been introduced in other states but does not appear to be established.	Arnett et al., 2002; Müller-Schärer and Schroeder, 1993; http://www.biocontrol.entomology.cornell.edu/weedfeed/Cyphocleonus.php
Cyrtepistomus	*castaneus*	Roelofs, 1873	omajor	It is found in southern North American forest and grasland ecosystems, along with *Cryptorhynchus lapathi*. Both species are polyphagous and feed on various family plants. It feeds in Carya, Castanea, Cornus, Corylus, Fagus, and Quercus .It can be extremely common locally and is primarily found on Quercus spp. and Castanea spp., though it is considered a minor defoliator .	Frederic and Gering, 2006; Douglas et al., 2013
Diaprepes	*abbreviatus*	Linnaeus, 1758	minor	Feeds on a variety of ornamental plants grow in southern Florida (polyphagous). Plaguing citrus orchards and many ornamental plant species, has a host range of nearly 293 plant species (several native and ornamental). This weevil is native to the Caribbean region where it is an economic pest of many agricultural	O'Brien and Wibmer, 1982; Arnett et al., 2002; Frederic and Gering, 2006

				crops including citrus. Many growers have experienced a devasting effect on the tree caused by larval feeding injury to the roots, where trees are planted in poorly dried solids. This weevil infests ~ 60,000 ha of commercial citrus found in 20 Florida countries.	
Diocalandra	*taitensis*	Guér.	omajor	In Fanning and Washington islands, the most important coconut insect is a weevil, which bores into the fronds, trunks, spathes, and young nuts of healthy trees but not as a rule of trees less than three years old	McCoy et al, 2000; Diaz et al. 2006; http://entnemdept.ifas.ufl.edu/creatures/citrus/diaprepes_root_weevil.htm
Elleschus	*bipunctatus*	Linn.	minor	On the spring it can be found on catkins (long petal less flowers: willow tree, poplar, etc.). Specially associated with Salix spp. In Canada it was found in a small willow growing in upland thickets.	O'Brien and Wibmer, 1982; Herms, 1926
Euophryum	*confine*	Broun, 1880	minor	It tunnel structural softwoods and hardwoods undergoing fungal decay, but most commonly the Scots pine (*Pinus sylvestris);* association with *Coniophora puteana* (cellar root), *Serpula lacrymans (dry rot),* and *Antrodia (Fibroporia) vaillantii (white rot).* Outdoors they are found In trees and logs decayed by a wide range of brown and white rot fungi. In the UK it has been found in both building timbers and decayed wood in the wild. Found in Canada Newfoundland (insular)	Cooter and Barclay, 2006; Aukema et al. 2010
Euscepes	*postfasciatus*	Fairmaire, 1849	minor	Sweet potato and wild species in the genus Ipomoea. In Japan, these specie and *Cylas formicarius* pests are distributed only in Ryukyu Islands and Bonin Islands, the southernmost part of the Japanese territory, and movement from infested areas to uninfested areas of host plants of the pests is strictly prohibited, based on Japan's Plant Protection Law.	Green and Pitman, 2001; Langor et al. 2009
Graphognathus	*leucoloma*	Boheman	minor	Able to feed on a very wide range of plant species. It causes most severe damage in the following: *Brassica spp., Daucus carota, Fragaria x ananassa, Medicago sativa, Pisum sativum, Rubus spp., Solanum tuberosum, Trifolium spp.* and *Zea mays*. Pastures can be seriously damaged, with the legumes and not the grasses being attacked. *N. leucoloma* has been recorded on 385 species in the USA alone (Young et al., 1950), including, besides the above-mentioned, various herbaceous crops such as *Arachis hypogaea, Ipomoea batatas* and *Vigna unguiculata*, weeds, grapevine and	O'Brien and Wibmer, 1982; Moriya and Miyatake, 2001

				trees such as *Prunus persica* (peach) and Salix (willow). Also known *as Naupactus leucoloma* or *Pantomorus leucoloma*. Adults have been reported in 140 different hosts	
Graphognathus	*minor*	Buchanan	minor	Generally distributed in the south-eastern United States. Adults are considered pests and feed on foliage of various plants. Also known as Naupactus, Asynonychus, Mimopactus, Archopactus. This species and two others (*N. leucoloma* (Buchanan) and *N. peregrinus* (Buchanan)) comprise the whitefringed beetle complex in North America. Whitefringed beetles are considered serious pests of many agricultural crops and have become pests of young pines planted on converted croplands in the South. Whitefringed beetles have been associated with over 385 plant species. The most common hosts are cotton, peanuts, okra, velvetbeans, soybeans, cowpeas, sweet potatoes, beans, and peas. Adults seem to prefer plants with large, broad, smooth leaves; larvae feed on agricrop plant roots, newly germinated acorns and nuts, and the roots of woody plants (e.g., peach, pecan, tung, willow) and pines.	O'Brien and Wibmer, 1982; http://entnemdept.ufl.edu/creatures/orn/beetles/fuller_rose_beetle.htm
Graphognathus	*peregrinus*	Buchanan	minor	Generally distributed in the south-eastern United States. Adults are considered pests and feed on foliage of various plants. Also known as Naupactus, Asynonychus, Mimopactus, Archopactus. This species and two others (*N. leucoloma* (Buchanan) and *N. minor* (Buchanan)) comprise the whitefringed beetle complex in North America. Whitefringed beetles are considered serious pests of many agricultural crops and have become pests of young pines planted on converted croplands in the South. Whitefringed beetles have been associated with over 385 plant species. The most common hosts are cotton, peanuts, okra, velvetbeans, soybeans, cowpeas, sweet potatoes, beans, and peas. Adults seem to prefer plants with large, broad, smooth leaves; larvae feed on agricrop plant roots, newly germinated acorns and nuts, and the roots of woody plants (e.g., peach, pecan, tung, willow) and pines.	Arnett et al., 2002

Heilus	*bioculatus*	Boheman 1943	minor	Found in southern Florida. Adults and larvae have been associated with *Bursera simaruba* (l.) Sarg. (Burseraceae)	Arnett et al., 2002; Lanteri and Marvaldi, 1995
Hypera	*postica*	Gyllenhal, 1813	minor	Exotic Insects which have become major pests in the US agriculture. Is a destructive pest of alfalfa (Lucene) and few closely related legumes. Was first detected in North America in 1904 in an alfalfa filed a few kilometres from Salt Lake City, Utah.	Arnett et al., 2002; www.plantwise.org/KnowledgeBank/Datasheet.aspx?dsid=28335
Hypera	*rumicis*	Linnaeus, 1758	minor	*H. exemius*, which was formerly known as *H. rumicis* (these two names possibly being synonymous) and which occurs mainly on dock (*Rumex crispus* and *Rumex mexicanus*) and is of no economic importance. However is well distributed throughout the United States on rhubarb and several species of dock, but has not been of economic importance until it was found causing serious damage to the leaves and blossoms of sorrel (*R. acetosella*) grown for seed in Connecticut.	O'Brien and Wibmer, 1982; Arnett et al., 2002
Isochnus	*populicola*	Silfverberg, 1977	minor	Larvae mine leaves of willow (Salix) and poplar (Populus): pupation takes place in mine. Adults found on larval hosts plants.	O'Brien and Wibmer, 1982; Munson and Enns, 1968; Arnett et al., 2002
Larinus	*planus*	Fabricius 1792	omajor	It have been introduced for the biological control of *Cirsium arvense* (L.) Scop. (Canada thistle), and *Centaurea solstitialis* L. (yellow star-thistle), *C. maculosa* Lam. (spotted knapweed) and *C. diffusa* Lam. (diffuse knapweed) (all Asteraceae).This insect was introduced accidentally at some time before 1968 into the north-eastern United States, where it is now widespread in Pennsylvania, Maryland, Ohio and New York. It is not recorded from Canada. L. planus is recorded in Europe mainly from *C. arvense* and *C. palustre*, although there are occasional breeding records from a number of other Cirsium and Carduus spp. It generally prefers thistle with small flower heads. It is causing a serious reduction in the number of seeds produced by a native North American Cirsium species, such as Tracy's thistle.	Aukema et al. 2010; Bright and Bouchard 2008
Listroderes	*costirostris*	Schoenherr	minor	South eastern United States, Texas, Arizona and Califorina; adventive. Is the senior synonym of *Listroderes difficilis*and *L.obliquus* (junior synonym). It is extremely polyphagous, feeding on a wide range of cultivated and wild	Arnett et al., 2002; Friedman, 2009; Clancy, 1969

				plants, affecting all parts of the host plant at both the larval and adult stages.	
Macrorhyncolus	*littoralis*	Broun, 1880	minor	Found in California. Adults are associated with driftwood on coastal beaches.	O'Brien and Wibmer, 1982; Arnett et al., 2002; Havens et al., 2012; McClay, 1989; Louda and O'Brien, 2002
Magdalis	*barbicornis*	Latreille 1804	minor	Cydonia, Malus. Associated with hawthorn (Crategus Tourn. ex. L., Rosaceae) and other members of the rose family. Adults are associated with various trees; larvae mine in bark of dead or dying trees. The preference of this weevil for wild and cultivated members of Rosaceae may indicate a potential threat to California agriculture and natural forest ecosystems. However, 35 years have passed since the original collection of the species in California, and no significant damage by this weevil has been reported during that time period	Sauvard et al. 2010
Mesites	*spp.*		minor	Found in eastern United States. Species are associated with driftwood on Atlantic and Gulf Coast beaches.	O'Brien and Wibmer, 1982; Arnette et al., 2002; Aukema et al. 2010; Anderson and Cline, 2011
Metamasius	*callizona*	Chevrolat, 1883	major	This species is devasting native Florida (limited invasive range) bromeliad populations. Of Florida's 16 native bromeliad species, 12 are hosts for larvae of *M. callizona*, and eight species have been found infested in the wild. Ten of the 16 native bromeliads are endangered or threatened. Bromeliads are considered ecosystem engineers because they create habitats, which are inhabited by many invertebrates (). So, any extinction of native bromeliads could reduce invertebrate biodiversity and alter biochemical cycles.	Frank and Thomas, 1994; Cooper, 2008; Frank and Fish, 2008; Cooper et al., 2011; Cooper et al., 2014
Metamasius	*hemipterus*	Linnaeus, 1758	minor	Is associated with palms, sugar cane and bananas. Major hosts of M. hemipterus are Cocos nucifera (coconut), Musa (banana) and Saccharum officinarum (sugarcane), but the pest has also been recorded on other plants such as Ananas comosus (pineapple), Manihot esculenta (cassava), Sorghum bicolor (sorghum), Zea mays (maize), Carica papaya (papaya), Psidium guajava (guava), as well on many palm species (Bactris gasipaes, Hyophorbe verschaffeltii, Iriartea ventricosa,	Arnett et al., 2002; Ramirez-Lucas et al. 1996; Perez et al. 1997; Woodruff and Baranowski, 1985; Kanzaki et al. 2008; http://entnemdept.ufl.edu/creatures/orn/silky_cane_weevil.htm

				Jessenia bataua, Phoenix canariensis, Ptychosperma macarthurii, Ravenea rivularis, Roystonea borinquena, R. regia, Washingtonia robusta). There is no indication from the literature of whether date palm (Phoenix dactylifera) is a host plant of M. hemipterus. Is a pest in Central ando South America, the Caribbean and Africa. In the mid-1980s the weevil was introduced into Florida, where it has become a significant pest of ornamental palms and sugarcane. In Colombia as a possible vector of the nematode, Bursaphelenchus cocophilus, responsible for red ring disease in oil palm.	
Microlarinus	*lareynii*	Jacquelin du Val	minor	Founded in southwestern United States and Washington. Adults have been introduced for the biological control of *Tribulus terrestris* L. (puncturevine; Zygophyllaceae). Field and laboratory studies conducted in France, Italy and California during 1959-1961 demonstrated that the adults fed on a wide range of plant species, but reproduction succeeded only on puncture vine, other species of Tribulus, and a few herbaceous annual Zygophyllaceae native to the southwestern United States	O'Brien and Wibmer, 1982; http://invasives.wsu.edu/biological/microlarinuslareynii.htm ; http://www.faculty.ucr.edu/~legneref/biotact/ch-88.htm ; Arnett et al., 2002 ; http://www.faculty.ucr.edu/~legneref/biotact/ch-88.htm
Microlarinus	*lypriforms*	Wollaston	minor	Founded in southwestern United States and Washington. Adults have been introduced for the biological control of *Tribulus terrestris* L. (puncturevine; Zygophyllaceae). ield and laboratory studies conducted in France, Italy and California during 1959-1961 demonstrated that the adults fed on a wide range of plant species, but reproduction succeeded only on puncturevine, other species of Tribulus, and a few herbaceous annual Zygophyllaceae native to the southwestern United States	O'brien and Wibmer, 1982; Arnett et al., 2002; http://www.faculty.ucr.edu/~legneref/biotact/ch-88.htm
Mogulones	*cruciger*	Herbst, 1784	minor	Found in British Columbia and Alberta. This species has been introduced for the biological control of *Cynoglossum officinale* L. (hound's-tonge; Boraginaceae). Was first released in Canada in 1997 to control that weed. Its host-specificity tests show associated risks to native confamilial plant species. The weevil developed in host-specificity tests on *H. floribunda*, *L. squarrosa* and five *Cryptantha* species closely related to *C. spiculifera*. Permission the fundamental host range of M. cruciger as determined from pre-release host-specificity tests, and associated risks to native confamilial	Arnett et al., 2002; De Clerck-Floate et al. 2005; Andreas et al. 2008; De Clerck-Floate and Schwarzländer, 2002

				plant species. With large populations close to the northwestern US border, M. cruciger has begun to migrate south into the US. Based on its known oligophagous fundamental host range within the Boraginaceae. M. cruciger is an oligophagous species that can complete development on species within closely-related genera in the Boraginaceae, but still prefers houndstongue as a host.	
Myllocerus	*undatus*	Marshall	omajor	It has been recorded in 68 different hosts in Florida.	O'Brien et al. 2006; Epski et al. 2009; http://www.freshfromflorida.com/Divisions-Offices/Plant-Industry/Plant-Industry-Publications/Pest-Alerts/Pest-Alerts-Myllocerus-Undatus-Marshall
Myosides	*seriehispidus*	Roelofs 1873	minor	Found in Maryland, Massachusetts, Connecticut, New York, Ohio, Rhode Island and West Vircinia. It was reported in the Great Smoky Mountains National Parl (GSMNP). Is a small broadnose weevil from Japan, reported as established in the eastern US since at least 1973. The life history of the species is poorly known and its potential status as a pest of native and/or cultivated plants, mode of dispersal, and other biological details are unknown.	Carlton and Anderson, 2004; O'Brien, 2000; http://entnemdept.ufl.edu/creatures/orn/sri_lankan_weevil.htm
Otiorhynchus	*meridionalis*	*	minor	Minor pest in the Mediterranean basin. Adults feed on the leaves and flowers of various members of the Oleaceae, including cultivated olive. In North America is damaging to lilac, but also feed on a wide variety of other plants (e.g. peony --> some native to Western North America, privet). It occurs in the western US, from California to New Mexico, north Washington and Montana; it is not yet recorded from Canada. On California privet, Ligustrum ovalifolium and Ligustrum vulgare.	O'Brien and Wibmer, 1982; Aukema et al. 2010; Heijerman and Hellingman, 2009
Otiorhynchus	*ovatus*	*	omajor	Polydrusus sericeus, Phyllobious oblongus, and Sciaphilus asperatus, Barypeithes pellucidus, Calomyceterus setarius, Otiorhynchus ovatus, Pachyrhinus elegans, Strophosoma melanogrammum, and Trachyphloeus aristatus composed the >80% of the total individual weevils collected in North American northern hardwood forests. These last six species are	Pinski et al., 2005

				less abundant although they may be contributing at the displacement of native species of weevils in native ecosystems	
Otiorhynchus	*porcatus*	Herbst	minor	In North America it has been recorded from *Syringa* sp. (Oleaceae) and *Viburnum* sp. (Caprifoliaceae). Potential host plants of the Otiorhynchus porcatus at the green roof site in Halifax would appear to be: Solidago canadensis and S. rugosa, given that Otiorhynchus porcatus has adapted to feed on Solidago altissima, an adventive plant introduced to Europe from North America; Lonicera canadensis, closely related to the genus Viburnum in the Caprifoliaceae, a host recorded in Canada by Campbell et al. (1989); and, Lysimachia punctata, closely related to the genus Primula in the Primulaceae, a known host plant in Europe. No plants in the Saxifragaceae, Rosaceae, or Oleaceae were found at this site, although there were three other species in the Asteraceae in the genera Aster and Leucanthemum.	O'Brien and Wibmer, 1982; Majka and MacIvor, 2009
Otiorhynchus	*singularis*	Linnaeus	minor	Occurs in the eastern and western portions of North America. Is a serious pest of raspberry and other small fruits, ornamentals, and seedling conifers. Other plants attacked by this species in North America include apple, campanula, holly, iris, laurel, primrose, rhododendron, and strawberry. The species was first recorded in north America in 1872 from Essex, Mass.	O'Brien and Wibmer, 1982; Aukema et al., 2010; Bright and Bouchard, 2008; http://www.plantwise.org/KnowledgeBank/Datasheet.aspx?dsid=38070
Otiorhynchus	*sulcatus*	Fabricius	minor	Polyphagous insect. Over 150 species of an even more expansive list has been recorded, altough in it has not been demostratet that all are viable hosts. Picea, Rhododendron, Takus, Tsuga. Also known as *Brachyhincus sulcatus*. O. sulcatus continues to be a serious pest of Taxus and hemlock trees (Tsuga), especially in nurseries in Connecticut, USA, and also attacks rhododendrons (Schread, 1966). O. sulcatus caused injury to Concord grapes in south-central Washington, USA, by feeding on the berry pedicels and cluster stems.According to Morris (1997), O. sulcatus is very highly polyphagous and a pest of house plants, garden, greenhouse and orchard crops, as well as vines (in continental Europe).	O'Brien and Wibmer, 1982; Van Tol et al. 2012; http://www.cabi.org/isc/datasheet/38071

Pachyrhinus	*elegans*	Schoenherr	omajor	*Polydrusus sericeus, Phyllobious oblongus*, and *Sciaphilus asperatus, Barypeithes pellucidus, Calomyceterus setarius, Otiorhynchus ovatus, Pachyrhinus elegans, Strophosoma melanogrammum*, and *Trachyphloeus aristatus* composed the >80% of the total individual weevils collected in North American northern hardwood forests. These last six species are less abundant although they may be contributing at the displacement of native species of weevils in native ecosystems.	Pinski et al., 2005
Pantomorus	*tessellatus*	Say, 1824	omajor	Also known as *Aramigus tessellatus* (Say, 1824) and *Partonomus pallidus*. Is naturally distributed in Argentina, Brazil, and Uruguay, but with a wider and more southern distribution. It's considered to have been introduced into central Chile, Mexico and United States, where it occurs from Nebraska, Iowa, and Illinois in the north to Texas in the south. Is a pest of cereals such as wheat (*Triticum aestivum*), oat (*Avena sativa*), and barley (*Hordeum vulgare*). It also attacks lucerne, sunflower (*Helianthus annus*), and potato (*Solanum tuberosum*). It is also associated with raspberries (*Rubus spp.*) and pears (*Pyrus* spp.) in Chile and wild pastures in the United States.	O'Brien and Wibmer, 1982; Lanteri et al., 2013; http://www.coleoptera-neotropical.org/paginas/3_familias/CURCULIONIDAE/0ch/Aramigus-tessellatus.html
Philopedon	*plagiatum*	Schaller, 1783	minor	It is a large root weevil associated with sandy, coastal, habitats where it feeds on the roots of marram grass, *Ammophila breviligulata*. In North America it is restricted to Atlantic Canada. An introduced Palearctic weevil first recorded in North America in 1934 in the Iles de la Madeline, and thereafter found in New Brunswick, on Prince Edward Island, and in Nova Scotia. This species is polyphagous on numerous species of herbaceous plants and trees. It is reported attacking a variety of cultivated plants and trees but is of no economic importance in Canada. Widely distributed in Europe and mostly in sandy districts; also present in North Africa.	O'Brien and Wibmer, 1982; Majka and Shaffer, 2008; Bright and Bouchard, 2008; http://bugguide.net/node/view/460389
Phyllobius	*intrusus*	Komo	minor	North-eastern United States and adjacent Canada. Adults feed on foliage of various trees. It was identified from samples submitted by a retail nursery producing ornamental Thuja near Langley, in May 1994. Is known to feed on various ornamental cultivars of cedar (arborvitae), cypress and jupiter including the following species: Thuja occidentalis, T.	Arnett et al., 2002; Duncan, 1994; Ødegaard and Berggren, 2010

				orientalis, T. standishii, Chamaecyparis obtusa, C. pisifera, Juniperus chinensis, J. excelsa, J. virginiana. The suitability of native Cupressaceae (Thuja plicata, Chamaecyparis nootkatensis, Juniperus communis, J. scopulorum) as hosts for this weevil has yet to be determined in British Columbia. The species originate from Japan, but is widely distributed in the USA and Canada due to introduction with the host plants, Thuja spp.	
Phyllobius	*oblongus*	Linnaeus	major	Dominant species (with *Polydrusus sericeus*) in North American northern hardwood forests. Together with *Sciaphulus asperatus*, set up a complex of non-indigenous root-feeding weevils that may be displacing the native weevil species.	Pinski et al., 2005
Polydrusus	*impressifrons*	Gyllenhal	minor	Accidentally introduced into New York State early in the 20 century. Causes noticeable injury to the foliage of ornamental weeping willow in Niagara Falls, Ont. The beetles feed on the foliage of large number of plants but prefer birch, willow, poplar, apple and pear. Scattered individuals have on occasion been taken on elm, rose, linden, and black locust.	O'Brien and Wibmer, 1982; Aukema et al., 2010; http://esa.confex.com/esa/2012/webprogram/Paper68335.html
Polydrusus	*sericeus*	Schaller	major	Dominant species (with *Phyllobious oblongus*) in North American northern hardwood forests. Together with *Sciaphulus asperatus*, set up a complex of non-indigenous root-feeding weevils that may be displacing the native weevil species.	Pinski et al., 2005
Pselactus	*spadix*	Herbst, 1795	minor	Acer, Salix. Codiosoma (Pselactus) spadix (Hbst.), a wood-boring weevil that often attacks timber associated with salt water (driftwood), was found in 1966 for the first time in California at Newark, under and in boards and timbers on levees above salt evaporation ponds	O'Brien and Wibmer, 1982; Aukema et al., 2010; Oevering and Pitman, 2002
Pseudocneorhinus	*bifasciatus*	Roelofs	minor	Found in eastern United States. Adults and larvae feed on wide variety of plants. Was first found in North America near Philadelphia in 1914, better known in the northeastern United States than in the Southeast. Most of the individuals have been recorded feeding in ornamental plants on private gardens. Other hosts recorded by Marrone and Zepp (1979) include azalea (Rhododendron), privet (Ligustrum), Forsythia, Abelia, Viburnum, Acer, Morus, Populus, Sedum, Lythrum, Campsis,	Allen, 1959; Schuder, 1969

				Thunbergia, and Coleus. Twobanded Japanese weevils are especially found in cherry laurel (*Prunus laurocerasus*), Pyracantha, Euonymus, barberry (Barberis) (Day 2003). Other hosts include ash (Fraxinus), burr marigold (Bidens), Camellia, dogwood (Cornus), elm (Ulmus), fern, hemlock (Tsuga), holly (Ilex), lilac (Syringa), mountain laurel (Kalmia latifolia), rose (Rosa), Spirea, strawberry (Fragaria), Weigela, Koelreuteria, and Deutzia.	
Rhinocyllus	*conicus*	Froelich	minor	Has been used for classical biological control of Cardus species in Argentina, Canada and the United States. It have had non-target impacts, which have raised safety concerns for native thistle plants. Concern exists over the feeding of this weevil on at least 25 species of native Cirsium thistles. It completed development in heads of the native species *C. carolinianum* (Walter), and *C. horridulum* Michaux, and significant reductions in seed numbers of the both species in 2008.	O'Brien and Wibmer, 1982; Wiggins et al., 2010; Cripps et al. 2011; http://www.cabi.org/isc/datasheet/47083 ; http://www.biocontrol.entomology.cornell.edu/weedfeed/Rhinocyllus.php
Rhinoncus	*perpendicularis*	Reiche 1797	minor	Three species adventive. Species are associated with *Polygonum* (Polygonaceae). It is known from only one locality near Ottawa, Ontario, where it was collected by sweeping *Polygonum hydropiper* L.	Anderson and Korotyaev, 2004; Hoebeke and Whitehead, 1980; Bouchard et al. 2005
Rhynchaenus	*rufipes*		omajor	A list is given of 16 trees and plants on which the adults feed when growing near willow, their principal food-plant. The larvae confine their attack almost entirely to willow, but have occasionally been found on poplar. *S. pentandra* is invariably the species most seriously mined, but in addition to native willows, *S. babylonica* is also attacked. It has been previously recorded in various parts of US on *Salix lucida*, and on *S. pentandra* in Canada. In New Jersey is known to occur on *S. lucida* and *S. nigra*	Nash, 1934; Weiss and Lott, 1921
Rhynchaenus	*rufitarsis*	Germar	minor	Is apparently increasing in Utah, where is recorded from Salix spp., *Populus angustifolia* and *Betula fontinalis*.	O'Brien and Wibmer, 1982; Jones, 1922
Rhynchophorus	*ferrugineus*	Olivier, 1790	minor	Occurs from Pakistan eastwards to Taiwan and the Philippines, also found in Saudi Arabia and the United Arab Emirates. Is present in California and there are some other restricted distributions on the USA. Its primary hosts include 24 species of palms in 14 genera (ornamental in California). Of potential concern	http://cisr.ucr.edu/red_palm_weevil.html http://cisr.ucr.edu/red_palm_weevil.html http://forestpests.org/vd/18041.html

				in the US is the risk to native palms in the genera Washingtonia and Sabal.	http://www.cabi.org/isc/datasheet/47472
Sciaphilus	*asperatus*	Bonsdorff	major	Together with *Polydrus sericeus* and *Phyllobious oblngus*, set up a complex of non-indigenous root-feeding weevils that may be displacing the native weevil species.	Pinski et al., 2005
Sitona	*lineatus*	Linnaeus	minor	First recorded in North America in 1936 from southern Vancouver Island, B.C. By 1942 the insect had spread to the interior of the province. The pea leaf weevil may cause serious injury to seedling peas, sweet peas, alfalfa, and clover. It also attacks broad beans, red clover, bird's-foot trefoil, wild and cultivated vetch, and has been found in threshed oats.	O'Brien and Wibmer, 1982; Bezemer et al. 2008; http://www.plantwise.org/KnowledgeBank/Datasheet.aspx?dsid=50230
Strophosoma	*melanogrammum*	Froster, 1771	omajor	Together with *Polydrus sericeus* and *Phyllobious oblngus*, set up a complex of non-indigenous root-feeding weevils that may be displacing the native weevil species.	Pinski et al., 2005
Tanysphyrus	*lemnae*	Fabricius, 1792	minor	It requires a host plant and is usually associated with duckweeds (*Lemna spp.*) and duckmeats (*Spirodela spp.)*. However, it can also be found on other species. For example, in Florida it is specifically associated with exotic water lettuce (*Pistia stratiotes*).	O'Brien and Wibmer, 1982: http://nas.er.usgs.gov/queries/GreatLakes/SpeciesInfo.asp?NoCache=12%2F10%2F2013+7%3A53%3A23+PM&SpeciesID=2363&State=&HUCNumber= ; http://invasions.si.edu/nemesis/CH-IMP.jsp?Species_name=Tanysphyrus+lemnae
Trachodes	*hispidus*	Linnaeus 1758	minor	Found in Newfoundland. Often associated with dead sticks. In woods, polyphagous on decaying wood (especially in hardwood, but occasionally softwood). The species is climatically quite undemanding and also occurs in higher altitudes, even if there is something rare. Distribution: Northern, Eastern and Central Europe, south to Romania. In Germany, widespread. Baden-Württemberg: Moderately common, detected in all parts of the country and high altitudes, something more common in	Arnett et al., 2002; Morris, 1991

				lower elevations. Hazard: widespread, usually not rare species, it is not at risk.	
Trachyphloeus	*aristatus*	Gyllenal	omajor	Together with *Polydrus sericeus* and *Phyllobious oblngus*, set up a complex of non-indigenous root-feeding weevils that may be displacing the native weevil species.	Pinski et al., 2005
Trachyphloeus	*bifoveolatus*	Beck, 1817	minor	Recorded from Barneveld, New York, New Brunswick and Nova Scotia; it has subsequently been taken in Otario in 1949. This weevil breeds in untended grassland fields and pastures (*Cladanthus mixtus, Pilosella officinarum, Plantago lanceolata, Fagus, Lotus, Knautia, Trifolium, Achillea, Rubus, Hieracium pilosella, Fragaria, Dianthus*). Can be a nuisance to homeowners when adults migrate in the autumn and spring. Adults feed on the foliage and crowns of plants; the larvae feed on roots. Is reported to be a common pest of grasslands, raspberries and vineyards.	O'Brien and Wibmer, 1982; Arnett et al., 2002; Aukema et al., 2010; Bright and Bouchard, 2008
Trichosirocalus	*horridus*	Panzer	minor	*Trichosirocalus horridus* Panzer (Coleoptera: Curculionidae), the rosette weevil introduced into North America against Eurasian thistles, feeding on native tall thistle, *Cirsium altissimum* L. Spreng., in tallgrass prairie. Established in Australia for biological control.	O'Brien and Wibmer, 1982; Takahashi et al., 2009; Kok, 1986; Woodburn, 1997; http://www.biocontrol.entomology.cornell.edu/weedfeed/Trichosirocalus.php
Tropiphorus	*terricola*	Newman	minor	Was first collected on the continent (NA) in Truro, Nova Scotia in 1913 followed by specimens from Québec City in 1917, and Charlottetown, Prince Edward Island in 1936. Inhabits wooded areas, open land and slopes. Adults have been reported to cause damage to strawberries and the crown and leaf stem on newly set, small in Nova Scotia. It occurs from Quebec to Newfoundland.	O'Brien and Wibmer, 1982; Aukema et al., 2010; Bright and Bouchard 2008; Majka and Anderson, 2007
Tropiphorus	*obtusus*	Bonsdorff 1785	minor	Found in Newfoundland, Nova Scotia and Quebec. First found on 1933. Associated with damp, shaded habitats, often along streams in woodlands or alpine areas, where they can be found under stones or plants. It has been collected in association with *Leontodon autumnalis* L. (Asteraceae), *Rumex acetosa* L. (Polygonaceae), and *Mercurialis perennis* L. (Euphorbiaceae). Is widely distributed in	Majka and Anderson, 2007

				central and northern Europe from France and Italy, north to Norway and Sweden, east to Poland, Lithuania, Estonia, and the St. Petersburg region of Russia, and south to Bulgaria and Romania as well as in Great Britain and Iceland.	
Anoplophora	*glabripennis*	Motschulsky, 1853	major	Its larva kills threes by tunnelling in the wood and the cambium. This species has a broad range of hosts that includes maple (Acer), buckeye/horse chestnut (Aesculus), birch (Betula), willow (Salix), and elm (Ulmus), where most of the infestations have been on urban forests and trees. Moreover, not much is known of *A. glabripennis* damages in forest ecosystems, although is considered a potential important threat, and it has been already found in several forest stands in and around Worcester, Massachusetts, United States.	Haack, 2006; Aukema et al., 2010; Nowak et al. 2001; Schloss et al. 2006; Dodds et al. 2014; Berland and Elliott, 2014; Sánchez and Keena, 2013; Podgwaite et al. 2013; Shatz et al. 2013
Callidiellum	*rufipennis*	Motschulsky, 1860	omajor	In its native range is known to feed on dead or dying trees, nevertheless it has been found on apparently healthy trees in Connecticut. It mainly feeds on dead or dying coniferous trees of the families Cupressaceae and Taxodiaceae, such as Chamaecyparis, Cyptomeria, Cupressus, Juniperus, and Thuja (Di Iorio, 2004; Haack, 2006)	Haack, 2006; Di-Iorio, 2004; Maier, 2009; Aukema et al., 2010
Crypturgus	*pusillus*	Gyllenhal	minor	Also known *as Bostrichus pusillus, Crypturgus atomus, Bostrichus aphodiodes, C. gaunersdorferi, C. crebellus, C. danicus, Polygraphus minimus*. Known hosts: Pinaceae: Abies sp., *Cedrus deodara, C. libani, Picea glauca, P. rubens, Pinus strobus*. In Canada is considered secondary, so it attacks trees that have previously harboured other bark beetle species such as *Ips typographus* and *Pityogenes chalcographus*. It very rarely attacks live trees. In Europe is associated with at least 15 fungi in the Ophiostomatoid group. It was introduced into the eastern US in 1868, New Brunswick in 1910, Nova Scotia in 1911, Prince Eduard Island around 1976, and Newfoundland. Its known host in Michigan are Pinus sp.	Haack and Rabaglia, 2013; Aukema et al., 2010; Cognato et al. 2009; http://www.barkbeetles.info/regional_chklist_target_species.php?lookUp=1868 ; http://www.exoticpests.gc.ca/es-details/insect/1000192
Gracilia	*minuta*		minor	Minor in the US. Main hosts: Salix Quercus, Rhamnus, etc. Has become sub cosmopolitan. Present in North America and North Africa. In Europ the larvae develops perfectly in plants of the genus Salix, although is polyphagous and lives on other genus like Quercus, Betula, Castanea, Rubus, Rosa, Corylus, Rhamnus,	Linsley 1959; Garcia, 2005; Di Iorio, 2004

				Ceratonia, Tilia, Ulmus, Ficus, Citrus, Malus and Morus. Also introduced in Argentina and Uruguay.	
Hylastes	*opacus*	Erichson	minor	Now also found in Oregon. In the USA, it has been collected from recently cut pine stumps and logs. It usually breeds in stumps and roots of dead or dying pines and occasionally other conifers. No reports of economic damage. The main hosts are *Pinus* but it can infest *Larix* and *Picea*. Also reported from Canada (Quebec, Ontario) and, as established, in South Africa. Its known hosts are Larix spp, Picea spp, Pinus resinosa, Pinus sylvestris, Pinus spp.	De Groot and Poland, 2003; Aukema et al., 2010; http://www.barkbeetles.info/regional_chklist_target_species.php?lookUp=399
Hylotrupes	*bajulus*	Linnaeus	minor	Minor in US. Structural insect pest of world-wide importance, as this species has been introduced from Europe to all major continents. The larvae infest and damage most of the common seasoned coniferous timbers used in buildings. It develops only in coniferous softwood. It is adapted to reinfest previously damaged wood, making use of breeding material for several generations.	Di-Iorio, 2004; Mattson et al 1994, Linsley, 1964; Aukema et al., 2010; Fettkother et al. 2000
Hylurgops	*palliatus*	Gyllenhal, 1813	minor	Hosts: All coniferous species (*Abies alba, A. nordmanniana, A. siberica, Cedrus sp, Larix gmelinii, L. siberica, Picea abies, P. excelsa, P. glehnii, P. jezoensis, P. koraiensis, P. koyamai, P. microsperma, P. obovata, P. omorika, P. orientalis, Pinus cembra, P. leucodermis, P. mugo, P. nigra, peuce, P. pinaster, P. pinea, P. radiata, P. rotundata, P. siberica, P. strobus, P. sylvestris, P. uncinata*) except yew. It attacks fallen and standing trees, usually dead and those dying. It infests the lower part of stems with the thick bark. This species prefers shaded and moist conditions. Trapped first in Pennsylvania in 2001 and later in New York and Ohio. No damage reports. In Eurasia, its hosts are Abies, Cedrus, Larix, Picea and Pinus	Invasive.org (2015); Hoebeke et al. 2006; Schroeder, 1992; http://www.barkbeetles.info/us_canada_chklist_target_species.php?lookUp=409 ; http://www.cabi.org/isc/datasheet/28197
Hylurgus	*ligniperda*	Fabricius	minor	It was discovered in November 200 near Rochester, New York. Found in a Christmas tree (*Hylurgus ligniperda*) plantation. Is best known for attacking stumps, freshly cult logs, and recent logging slash. Because of this behaviour, it might not appear to be a serious threat to North American forestry. However, the species has proven ability to spared globally and has a large host range including	Invasive.org (2015); Aukema et al., 2010

				pine species, spruce, true firs, Douglas fir, and larch. And *L. trucantum* has been reported from Canada and *L. procerum* has been implicated in white pine root decline the US.	
Orthotomicus	*erosus*	Wollaston, 1857	minor	*Orthotomicus erosus* is capable of infesting many species of pines. Its successful introduction into five other countries illustrates its ability to adapt to new hosts. Chararas (1973) reported that in Turkey, *O. erosus* was reared on a variety of hosts, including several North American pines. *Orthotomicus erosus* breeds in a large number of pines throughout its natural range. Several North and Central American pines that have been planted in areas where this insect is native or has become established, including Coulter pine, *Pinus coulteri*; Caribbean pine, *Pinus caribaea*; shortleaf pine, *Pinus echinata*; Monterey pine, *Pinus radiata*; Mexican weeping pine, *Pinus patula*; and Eastern white pine, *Pinus strobus*. Occasionally, maturing beetles feed in Douglas-fir, *Pseudotsuga menziesii*, Spruce, Picea spp.; Fir, Abies spp.; and Cedar, Cedrus spp. A host testing o 22 conifer species found in NA showed that larvae can develop in all pine species tested. It has invaded California and colonizes several species in the genus Pinus. Also found in South Africa, and associated with *Ceratocystis ips* in this region, but also with *Verticicladiella alacris* in pines. Usually breeds in recently fallen or cut trees and branches but it can colonize and kill live trees especially those stressed by drought, fire or wind.	Invasive.org (2015); Wingfield and Marasas, 1980; Tribe, 1992; Haack, 2004; Walter et al. 2010; http://www.cabi.org/isc/datasheet/37954
Pityogenes	*bidentatus*	Herbst	minor	It was firstly found in a nursery plantation of Bosnian pines in New York in early April 1988. In 2002, it was also found in Pennsylvania. The main host is *Pinus*, but *Abies, Larix, Picea* and *Pseudotsuga* can also be infested. In New York, it has been reported from both *Pinus* trees and logs. Is a common in conifer forests and northern Europe and colonize Scots pine, *Pinus sylvestris*. It appears to be a "nonaggressive" species, rarely attacking living trees, but specializing in colonizing diseased and dying branches.	Aukema et al., 2010; Byers et al. 2000; Hoebeke, 1989;

Scolytus	*mali*	Bechstein, 1805	minor	Synonyms: *Scolytus mali, Bostrichus mali, Eccoptogaster castaneus, E. pruni, E. pyri, Scolytus sulcatus, S. nitidulus, S. mali strigilatus, S.bicallosus*. Attacks weakned *Malus pumila*, Pyrus, Sorbus, Prunus and Ulmus trees. Inner bark of recently killed boles and large branches of *Malus pumila* Mill. and *Ulmus americana*.	Invasive.org (2015); Aukema et al., 2010; http://msue.anr.msu.edu/news/new_bark_beetle_pests_in_michigan; http://www.barkbeetles.info/us_canada_chklist_target_species.php?lookUp=1144 ; http://idtools.org/id/wbb/bbgus/Scolytus.htm
Scolytus	*multistriatus*	Marsham, 1802	major	It is considered the principle vector of the Dutch elm disease pathogen *Cerato cystisulmi*, which has devastated elm populations in north-eastern United States. It has been found that this true bark beetle attacks all native and introduced species of elms. However, it seems that this species has been recently displaced by *Scolytus schevyrewi*, another invasive true bark beetle.	Invasive.org (2015); Aukema et al., 2010; Pearce et al. 1975; Lee et al. 2011; Jacobi et al. 2013
Scolytus	*rugulosus*	Müller, 1818	omajor	Despite *S. rugulosus* is mainly a pest of orchards, damaging healthy trees, it has been recorded on several native *Prunus* species such as *Prunus americana*, *P. caroliniana*, P. mexicana, *P. pensylvanica*, and *P. serotia*, but also from trees in the genus shadbush (*Amelanchier*) and thorn apple (*Cartageus*).	Aukema et al., 2010; Kovach and Gorsuch, 1985; Doerr et al., 2008; Atkinson, 2014; http://www.barkbeetles.info/regional_chklist_target_species.php?lookUp=1170
Scolytus	*schevyrewi*	Semenov	omajor	It also transmits the Dutch elm disease to healthy native elms, although it seems not to be very efficient (Jacobi et al., 20013). *Scolytus schevyrewi* seems to be displacing another invasive species, *Scolytus multistriatus*. It is widespread in most of the states of the US and is also now found in Canada. It is known to colonize and kill stressed elms, and may vector a fungal species that causes Dutch elm disease.	Aukema et al., 2010; http://msue.anr.msu.edu/news/new_bark_beetle_pests_in_michigan; Smith and Clayton, 1970; Nickle, 1971; Doerr et al., 2008; Jacobi et al. 2013; Lee et al., 2010; Lee et al. 2011; Smitley, 2011; CABI, 2015
Sybra	*alternans*	Wiedemann	minor	Minor in the US? Main hosts: Ficus spp. (Florida strangler fig). No NZ interceptions made. Native to Asia Pacific, and introduced to Florida. First detected on early 1990s. It has nocturnal activities and seems to prefer host plants that are thoroughly dried. The beetle feeds on the inner fermenting and decaying bark and the outer wood. It was distributed to Indonesia, Philippines, Micronesia, and Hawaii Islands. It hast a wide host range including dry limbs of live fig tree, stems of jack beans, dead aerial root of Pandanus, dead stems of most	Haack, 2006; Aukema et al., 2010; Grebennikov et al. 2010; Chen et al. 2000

				kinds of trees and shrubs of the lowlands, dead stems of basil and cocklebur, dead twigs of cotton, dead branch of breadfruit tree, pineapple, garden bean, Cordia fruits, dead Euphorbia plants, dying stems of *Euphorbia multiformis* and algaroba (Prosopis) trees, and have been reared from Hau (Hibiscus), dead branches of Artocarpus, Barringtonia, Cycas, Triphasia, peduncles of passion fruit, Hibiscus, Ficus, Cordia, pseudo bulbs of orchids sp, klu pods and its seed coats	
Tetropium	*fuscum*	Fabricius, 1787	major	Major in Canada. *Tetropium fuscum* was introduced and became established in eastern Canada in Halifax, Nova Scotia ca. 1990. The main area of infestation is Point Pleasant Park but infestations have also been detected outside of the Park. This insect is believed to have arrived in Halifax at least 10 years prior to its discovery via dunnage, wood packing material, or pallets on board ships coming from the insect's home range. Point Pleasant Park is adjacent to the container terminal of the Port of Halifax, where this wood packing material is piled on site. Other species of Tetropium have been intercepted in wood products entering North America, Europe and South America. Main host genera: Picea. In its native range attacks weakened Norway spruce, *Picea abies*, but in Nova Scotia, it is infesting and killing apparently healthy red spruce, *Picea rubens*; white spruce, *Picea glauca*; black spruce, *P. mariana*, and Norway spruce. Other conifers reported to be susceptible in Europe include *P. pungens, P. sitchensis, Abies alba, Pinus sylvestris*, and occasionally Larix spp. It is competing with the native species *T. cinnamopterum*, although the non-native species seem to have restricted range.	Invasive.org (2009); Sweeney et al. 2004; Rhainds et al. 2011
Tetrops	*praeusta*	L.	minor	Main hosts: Rosaceae and other hardwoods (twigs). No NZ interceptions made. Introduced to North-eastern USA and Quebec, its first detection in North America was in 1996	Haack, 2006; Aukema et al., 2010; Grebennikov et al. 2010
Tomicus	*piniperda*	Linnaeus, 1758	omajor	It has spread rapidly in the USA and Canada, and is one of the dominant Scolytinae species in north-eastern Ohio. *Tomicus piniperda* has been found infesting stressed native pine trees (*Pinusbanksiana*, *P. resinosa*, and *P. strobus*), and according with Byers (1992) it has	Invasive.org 2015; Aukema et al., 2010; Byers, 1992; Gandhi et al. 2010; Langor et al. 2009; http://entnemdept.ufl.edu/creatures/trees/beetles/pine_shoot_beetle.htm

				occasionally killed living Scots pine (*Pinussylvestris*).	
Trichoferus	*campestris*	Faldermann	minor	Iwata and Yamada (1990) indicated about 40 genera of woody spermatophyte plants, both conifers and angiosperms, as host plants for *T. campestris* and concluded that this species can potentially attack most woody plants. Švácha and Danilevsky (1988) reported that the larvae live under bark and in dry dead wood and complete their development in two or more years. Adults emerge from July to August and readily fly. Their known living hosts are Betula spp, Broussonetia spp, Gleditsia spp, Malus spp, Morus spp, Picea spp, Pinus spp, Salix spp, Sorbus spp, and other 30 genus of plants likely dry wood hosts. Also known as *Trichoferus turkestanicus* Heyden, *Trichoferus flavopubescens* (Kolbe), T*richoferus rusticus* Ganglbauer. It is a potential risk of all Canadian urban maple trees to colonisation by non-native wood boring insects.	Grebennikov et al., 2010; Bullas-Appleton, 2014

Table A.1.2 Non-native beetle established in New Zealand natural ecosystems.

Genus	Species	Species author	Impact level	Details	References
Aphela	*helopoides*	Pascoe 1865	minor	Feeds on driftwoodand, it could have indirect effects on native ecosystems via competition, and by changing chemical, physical, and/or structural biotope characteristics (Blackburn et al., 2014).	Kuschel, 1972; Phillips et al., 2008; Blackburn et al., 2014
Gerynassa	*sp.*	*	minor	Species found in native bush, probably as temporary hosts because of the widespread distribution of their exotic host plants	Kushel 1990
Listroderes	*costirostris*	Schönherr	minor	Species found in native bush, probably as temporary hosts because of the widespread distribution of their exotic host plants	Kushel 1990
Listronotus	*bonariensis*	(Kuschel 1955)	minor	South American weevil species, bores in grass stems as larvae and causes significant production losses in pastures, and is an economically important pest. Adults and larvae are oligophagous, feeding on a wide host range of Poaceae. Although this species prefers exotic hosts, such as Loliumspp., wheat and sweet corn , it has been collected in New Zealand native shrub land in Otago, also in two tussock grassland sites (Mt Benger and Deep Stream, in Otago), and on Cornet Peak.	Barker et al., 1989; Rowan et al., 1990; Williams et al., 1994; Derraik et al., 2001: McNeill et al., 2002; Murray et al., 2003; Barratt et al., 2007; Phillips et al., 2008; Plantwise, 2014
Macrorhyncolus	*littoralis*	(Broun 1880)	minor	Feeds on driftwood and, it could have indirect effects on native ecosystems via competition, and by changing chemical, physical, and/or structural biotope characteristics.	Phillips et al., 2008; Sauvard et al., 2010; Blackburn et al., 2014
Maleuterpes	*spinipes*	Blackburn 1893	minor	Australasian species, which is expanding its range around North Auckland and is also damaging the native Phebaliumnudum (Rutaceae).	Kuschel, 1972
Mesites	*pallidipennis*	Boheman 1838	minor	Feeds on driftwood and, it could have indirect effects on native ecosystems via competition, and by changing chemical, physical, and/or structural biotope characteristics.	Brockerhoff and Bain, 2000; Phillips et al., 2008; Blackburn et al., 2014
Naupactus	*cervinus*	Boheman 1840	minor	According to Brockerhoff and Bain (2000), this species attacks indigenous trees, but no other publications supporting this information were found. Fullers rose weevil larvaeare considered a threat to commercial kiwifruit orchards in New Zealand.	Brockerhoff and Bain, 2000; Logan et al., 2008
Pselactus	*spadix*	(Herbst 1795)	minor	Feeds on driftwood and, it could have indirect effects on native ecosystems via competition, and by changing chemical, physical, and/or structural biotope characteristics.	Brockerhoff and Bain, 2000; Oevering et al. 2001; Blackburn et al., 2014

Stenoscelis	*hylastoides*	Wollaston 1861	minor	Species found in native bush, probably as temporary hosts because of the widespread distribution of their exotic host plants	Kushel 1990
Stenoscelis	*diversipes lineata*	(Pascoe 1873)	minor	Species found in native bush, probably as temporary hosts because of the widespread distribution of their exotic host plants	Kushel 1990
Aridaeus	*thoracicus*	Donovan	minor	It has been found feeding on a dead native *Avicennia marina* spp. *australasic*, a mangrove tree found along creeks and estuaries in the North Island.	Brockerhoff and Bain, 2000; Dawson and Lucas, 2012

Table A.1.3 Non-native spiders established in North American natural ecosystems.

Genus	Species	Species author	Impact level	Details	References
Araneus	diadematus	Alexander, 1757	minor	Introduced in Canada. In North America, their range extends from New England and the southeast to California and the Northwester United States. They can also be found of southern Canada adjacent to the United States. It lives in grasslands and requires some form of moisture. This is an abundant spider in yards, gardens, farms, orchards, urban and suburban areas throughout its North American range. It also frequents forest edges, riparian corridors, and old fields. Can be found low to the ground or high up (you can even find them on the outside of skyscrapers, as a result of the "ballooning" they do as spiderlings).	Paquin et al. 2010; http://animaldiversity.ummz.umich.edu/accounts/Araneus_diadematus/ http://www.spiders.us/species/araneus-diadematus/
Arctosa	perita	Latreille	minor	Introduced in Canada. In Europe, it is found in sand dunes and sandy heaths, where females make their silk-lined burrows. The British Columbia specimens were collected on open ground on Burnaby Mountain in late May. Found in Vancouver, British Columbia; Europe, Asia, and North Africa.	Dondale and Redner, 1983; Paquin et al. 2010
Badumna	longinqua	(L. Koch, 1867)	minor	Eastern Australia, New Zealand, USA, Uruguay. This species can be easily found living in tree trunks, rock walls and also is very common inhabiting synanthropic habitats, such as window frames, wall crevicesm inside or outside houses, and in urban parks. In North America, the species was recorded in woodlands and agroecosystems in California and Oregon, and recently observed in vineyard plantations.	Pompozzi et al., 2013; Simó et al. 2011
Brachypelma	vagans	(Ausserer, 1875)	minor	USA (FL). It is known to occur naturally from Veracruz and the Yucatan Peninsula south along the Gulf coast to north-eastern Costa Rica. In Florida, a population was found in a 40-acre citrus grove bordered by irrigation canals on the south and west. Although the ultimate effect of a naturalized tarantula in Florida cannot at this time be accurately predicted, it would be irresponsible to assume that they will not have a deleterious effect on native wildlife, although it has been recorded in the wild in Florida.	http://entnemdept.ufl.edu/creatures/misc/spiders/m_redrump.htm (Edwards and Hibbard, 1999); M'rabet et al. 2007; M'rabet et al. 2005; Dor et al., 2011; Edwards and Hibbard, 1999
Cheiracanthium	mildei	Kock	minor	Found in CA vineyards. Evidence from laboratory and field experiments suggests that it drives food web dynamics in the vineyard ecosystem, suppressing not only herbivores but also native spiders, most likely through intraguild predation, while the predatory impacts of native spiders appear to be weaker. It is dominant on the Napa Vineyards, but less abundant on the surrounding oak forests. Causing necrotising skin	Paquin et al. 2010; Spielman and Levi, 1970; Foradori et al. 2005; Corrigan and Bennett, 1987

				lesions on humans and animals. Commonly found in synanthropic habitats in eastern NA.	
Clubiona	lutescens		minor	Introduced in Canada. Distributed to the USSR-European part, Caucasus, Ural, N- & E-Kazakhstan, Siberia, Holarctic. Found in natural ecosystems (Outside). A Holarctic species, often cited from central Europe.	Paquin et al. 2010; Paquin personal comunication (2014); Mikhailoy, 1990; Roddy, 1966; Madsen et al. 2004; De Castro & Alberdi, 2002
Clubiona	pallidula	Clerck, 1757	minor	Introduced in Canada. It is found in British Columbia and Washington, and southern Ontario. It has been collected in shrubs, herbs, under bark, in mole burrows in the solid, in cultivated crops, and in houses.	Paquin et al. 2010; Roddy, 1966; http://bugguide.net/node/view/759793
Cryptachaea	blattea	Archer, 1946	minor	Introduced in Canada. It has been recorded from California, and it range has been described from Los Angeles County north to Alameda and Mariposa counties. It has become cosmopolitan, so it is also found in Chile, Saint Helena, Republic of Cape Verde, Portugal, Belgium, and New Zealand. Also known as *Achaearanea acoreensis, Achaearanea blattea, Achaearanea teja, Achaearanea gochares, Cryptachaea acoreensis, Dipoena blattea, Dipoena tubercula, Theridion acoreensis, Theridium albo-gullatum, Theridium blatteus, Theridium setiger, Theridium tuberculum*. Found in natural ecosystems in Canada.	Paquin et al. 2010; Berrian et al. 2010; Paquin personal comunication, 2014; Huber et al. 1999; http://keys.lucidcentral.org/keys/v3/theridiidae/key/Key%20to%20Theridiidae%20spiders%20of%20biosecurity%20importan/Media/Html/Cryptachaea_blattea_%28Urquhart_1886%29.htm
Dysdera	crocata	C. L. Koch, 1838	omajor	Inhabits synanthropic and semi-synanthropic habitats (Guarisco, 1999; Nedvěd et al., 2011), but it appears to be inhibiting the restoration by native arthropod species of the coastal sage scrub in California, impeding the spread of these species from the adjacent source areas (Longcore, 2003).	Burger et al., 2001; Longcore, 2003; Rezac, Kral and Pekar, 2008; Nedved et al. 2011; Guarisco, 1999
Enoplognatha	latimana		minor	Introduced in Canada. It is found on hedgerows, meadows, parks and gardens. Its web is located in low growing vegetation and made up with a three dimension network of threads. Widely distributed, being found in both North America and Eurasia, and North Africa. In North America it appears to be confined to the west coast. Here it ranges from northern California to central British Columbia. The earliest record it was in Seattle 1928.	Paquin et al. 2010; Oxford and Reillo, 1994; http://toutunmondedansmonjardin.perso.neuf.fr/EN/pages_EN/enoplognatha_ovata-latimana_EN.htm
Enoplognatha	ovata		minor	Recorded in Canada from overseas. It lives mainly in deciduous shrubs and trees. It is a common inhabitant of weedy vegetation along the north-eastern seaboard of	Dondale et al., 1994; Oxford and Reillo, 1994

				North America. Widely distributed, being found in both North America and Eurasia, and North Africa.	
Enoplognatha	thoracica		minor	Introduced in Canada. Found in natural ecosystems (Outside). Probably introduced in North America from Europe.	Paquin et al. 2010; Paquin personal comunication, 2014; Oxford and Reillo, 1994; Tan et al., 1999
Entelecara	acuminata		minor	Introduced in Canada. Found in natural ecosystems (Outside)	Paquin et al. 2010; Paquin personal comunication, 2014
Holocnemus	pluchei	Scopoli, 1763	omajor	Appears to be displacing the native *Latrodectus hesperus* (Chamberlin &Ivie) in urban areas in California (Burger et al., 2001; Houser et al., 2014)	Burger et al., 2001; Vetter et al. 2011; Houser et al. 2014
Latrodectus	geometricus	C.L. Koch, 1841	minor	Cosmopolitan. The Brown Widow spider prefers tropical climates, and is commonly found in the southeast United States where it was introduced. This spider can be found on many man-made structures in dark corners or crevices around houses, barns, fences, or anywhere a web will fit near the ground. The web contains a retreat structure or tunnel to allow the spider to hide or escape from predators. The Brown Widow spider feeds on insects, and is known to kill anything that gets tangled in its web. US present: FL, GA, SC, MS, AL, CA, AR, CO and TX (is expanding its distribution). Seems to prefer urban habitats and has a microhabitat preference that allows great prevalence in areas lacking suitable protection for other Latrodectus spp. reported from urban areas. In California is thought to be displacing *L. hesperus*.	Bibbs et al., 2013; Vink et al. 2011; Brown et al., 2008; Vincent et al. 2008
Lepthyphantes	leprosus	Ohlert	minor	Introduced in Canada. Found in natural ecosystems (Outside). Also found in Chile	Paquin et al. 2010; Paquin personal comunication, 2014; Maruski and Koponen, 2004; Topçu et al. 2005
Linyphia	triangularis	Clerck, 1757	omajor	Is a successful invader of both coastal and forest habitats in Maine, where the densities of native lipyhiids, such as the *Neriene radiate* (Walckenaer) and *Pityohyphantes costatus* (Hentz), have declined or been reduced in the presence of other non-native species (Jennings et al., 2002; Bednarski et al., 2010; Jakob et al., 2011). Several studies have shown that these invasive species have negative impacts on the native *Frontinella communis* (Hentz) causing competitive displacement by web invasion (Bednarski et al., 2010; Houser et al., 2014). Web invasion and occasional predation of the native species under natural conditions has been recorded by *L. triangularis* but this has not been	Jakob et al., 2011; Jennings et al. 2002; Bednarski et al., 2010; Houser et al., 2014; Houser et al. 2005

				demonstrated under laboratory conditions (Bednarski et al., 2010; Houser et al., 2014).	
Meriola	arcifera	Simon, 1886	minor	It has apparently been introduced into California, present in Santa Cruz Island. In the Mauna Kea Science reserve (Hawai'i) it may be having a negative effect on the Wekiu bug population.	Plantick and Ewing, 1995; Naughton et al. 2014
Metaltella	simoni	Keyserling, 1878	minor	Argentina, Brazil and Uruguay, USA (TX, LA, MS, AL, FL, CA, AB, NC). It has been collected in all the Gulf Coast states as well as Alberta, Canada. It was later discovered in several widely scattered localities from Los Angeles to San Diego, recently became apparent that now is widely distributed in urban southern California and can routinely be collected without much effort. One cause for concern about the presence of *M. simoni* in Florida is its potential effect on our only native amaurobioid, *Titanoeca brunnea* Emerton. Until recently, this seemed to indicate that *M. simoni* was displacing *T. brunnea*. All of the records of *M. simoni* from peninsular Florida have been since 1980, from situations similar to those previously reported for *T. brunnea*. However, the latter collections by Corey seem to indicate that the two species coexist. First collected in US in Louisiana in 1944. It has been collected under trash cans and rotting wood around southern California. They may also be found under logs, with the web attached to log and ground, under bark, under boards, and boxes, in crevices and corners in buildings, or, in the case of males, wandering around. Additional records of this spider have been made in Alberta, Canada.	Vetter and Rust, 2010; Valle et al. 2013; Edwards, 2004; Vetter and Visscher, 1994; http://entnemdept.ufl.edu/creatures/misc/spiders/metaltella_simoni.htm
Metellina	segmentata	Levi, 1980	minor	Introduced in Canada. Is the most common one found around Vancouver and Seattle. It is found in forests, clearings, sides of forests paths, parks, and hedgerows.	Paquin et al. 2010; Bradley et al., 2006; http://toutunmondedansmonjardin.perso.neuf.fr/EN/pages_EN/metellina_segmentata-mengei_EN.htm
Neriene	montana		minor	Introduced in Canada. Found in natural ecosystems (Outside)	Paquin et al. 2010; Paquin personal comunication, 2014
Nesticus	cellulanus	Clerck, 1757	minor	East coast of NA (NY, MA, ME, NS and QC) (Gertsch 1949, 1984. Related to the native *Nesticus silvestrii*, *N. cellulanus* is occasionally found in buildings. Records from FC (Canada) are the first cave records of *N. cellulanus* in North America and the same cave is the only confirmed North American locality for *F. fimitaria*.	Bradley, 2013; Moseley, 2007; Reeves, 1999

Oecobius	annulipes		minor	Cosmopolitan. Found in southern Californian coastal sage scrub. It has colonized undisturbed habitats across the Southwest. In Texas it has been found living on the walls of certain brick buildings. They not live in communal webs, instead these spiders have individual webs regularly spaced a few cm apart. Commonly found in oak in urban and natural stands in Texas	Burger et al., 2001; Santos and Gonzaga, 2003; Vincent and Frankie, 1985
Oecobius	navus	Blackwall, 1859	minor	Cosmopolitan. It thrives in buildings, found in walls corners. In North America it has been found across the continent, with most records in the South. They live on the ground, the bark of trees, and among rocks. Many records are from buildings, frequently greenhouses. I have often found them occupying the small depressions on the surface of concrete block walls. Considered among the most common human associated spiders. They often prey on small ants, flies, and other small insects. Bloger et al. (2008) found a positive association of the species with the non-native ant, *L. humile* that suggests an ecological link between these species (facilitation or predator-prey relationship). Is specially related with habitat fragmentation and can be displacing native species. It is a euryphagous predator locally specialised on the most abundant prey.	Bradley, 2013; Bloger et al., 2008; Voss et al. 2007; Nedved et al. 2011; Liznarova et al. 2013
Ozyptila	praticola		minor	Introduced in Canada. Typically it lives in the undergrowth, but sometimes it can be found under tree barks or on lower branches of trees. Crab spiders (who ambush their prey) feast on bees and butterflies more often, than on other insects. Found in Washington and Massachusetts. Its range is the Pacific and Atlantic coasts of United states. Is a widespread and common European species and its two North American coastal records (one specimen for each) success separate unintentional introductions into this continent. Also known as *Xysticus praticola* and *Oxytila praticola*.	Paquin et al. 2010; Dondale and Redner, 1975; http://enfo.agt.bme.hu/drupal/en/node/10961
Parasteatoda	tepidariorum	C. L. Koch, 1841	minor	Also known as *Achaearanea tepidariorum* and *Theridion tepidariorum*. Widespread on United States and Canada. Closely associated with buildings and other human structures. Typically more common outdoors, but they are sometimes found inside garages and sheds, as well. Also look for them in the tree holes, rock walls, woodpiles, and other sheltered situations. It is largely absent in wild situations except around and in outer chambers of caves, on dry mountain ledges, and on dry ledges of river bluffs.	http://www.spiders.us/species/parasteatoda-tepidariorum/ ; Mittmann and Wolff, 2012
Philodromus	dispar	Walckenaer, 1826	minor	Introduced in Canada. It is a philodromid crab spider found on trees and bushes, is found in a variety of wooded habitats including broad-leaved, mixed and coniferisen woods, thickets, hedgerows, scrub, gardens and it sometimes comes into houses. Is a widespread	Paquin et al. 2010; http://srs.britishspiders.org.uk/portal/p/Summary/s/Philodromus+dispar ; Wolff and

				European spider. Is diurnal, ambushing hunter that can also rapidly run along plant surfaces. Found in the more remote forest habitats at the Rocky Point, due to its potential for dispersal of this introduced species.	Gorb, 2012; Humble, 2000; Muchmore, 1980
Pholcus	muralicola	Maughan & Fitch, 1976	minor	It is known only from rock walls in a limited area of Kansas. It has been described as an opportunist predator. Mosquitoes, beetles, moths, thrips, ants and a spider (*Achaearanea tepidariorum*) were found in shrouds in the webs. One female and several young were usually found together in a web	Huber, 2005; Vink personal comunication, 2014
Simitidion	simile		minor	Introduced in Canada. Found in natural ecosystems (Outside). It lives on sand dunes and rock steppes, Holarctic (Galle and Urak, 2007)	Paquin et al. 2010; Paquin personal comunication, 2014;
Sitticus	pubescens		minor	Found in USA, Massachusetts (But also in NH and NJ). It has been known for over 50 years in the Boston area where it is common, for example, in the Harvard Yard. It has been recorded as one of the dominant species of the forests dominated by Acer rubrum and Ilex verticillata in the Black Rock forest, a nature reserve and research facility in New York. Also known as *Aranea pubescens*, *A. truncorum*.	Cutler, 1990; Richman et al. 2012; Ovtcharenko et al. 2014; Ovtcharenko et al. 2014; http://www.peckhamia.com/salticidae/salticidae.php?adres=specimen.php?id=9023
Spermophora	senoculata	Dugès, 1836	minor	Huber (2002) considered this species to be among the commonest spiders in the human buildings in the USA, but it also invaded natural habitats in the USA and southern Europe. It has a Holarctic distribution. Records of this species include the USA, southern Europe, northern Africa and East Asia. Recently reported in South America.	Huber, 2002; Nentwig and Kobelt, 2010; Vadell et al. 2005; Beatty, 2002
Steatoda	bipunctata	Linnaeus, 1758	omajor	Is displacing the native *Steatoda borealis*(Hentz) in urban areas (Nyffeler et al., 1986; Burger et al., 2001; Jennings et al., 2002; Taucare-Ríos, 2010; Jakob et al., 2011).	Jakob et al., 2011; Burger et al., 2001; Nyffeler et al., 1986; Taucare-Rios, 2010
Steatoda	grossa	C. L. Koch, 1838	minor	Cosmopolitan. In North America it has now been found in states along the east and west coasts as well as those bordering the Great Lakes. Specimens have also been collected in Colorado. It's found in and around homes and buildings, but occasionally found outdoors in other sheltered spots, such as in wood piles, under rocks and bridges, etc. Prey is any insect, spider, or other arthropod that becomes entangled in the web. It is possible that this spider is a specialist on "pillbugs" probably because both live near the ground and are nocturnally active. It also is reported to capture and prey upon other spiders, including the true black widow spiders.	http://bugguide.net/node/view/6932 http://www.spiders.us/species/steatoda-grossa/ http://ento.psu.edu/extension/factsheets/false-black-widow ; Graudins et al. 2002; Levi, 1961; Taucare-Rios, 2010;

Tegenaria	gigantea		minor	Also known as *Tegenaria duellica* (adult synonym). Introduced in Canada. It is among the most common spiders in Garry oak ecosystems and other parts of the Georgia Lowlands and Puget Trough, are found across southern British Columbia and south along the coast to southern Oregon. They are abundant west of the coastal mountain ranges and rare elsewhere in North America. It became established somewhat earlier on southern Vancouver Island BC. The sympatric species is found almost exclusively in British Columbia, Washington, and Oregon.	Paquin et al. 2010; Vetter et al., 2003; Binford, 2001; Baird and Stoltz, 2002
Theridion	bimaculatum	Linne	minor	Invasive in Canada from overseas. It occupies the herb layer of fields, marshes and bogs. Six specimens were collected by sweep-netting in grass and other low vegetation immediately beneath apple trees. Fist collected in Washington in 1956, it occurs in ground litter, shrubs (both Enoplognatha species) and grassy fields, but are commonest at sites heavily disturbed by human activity. It occupies the herb layer of fields, marshes and bogs. It has been collected in Meserole Apple Orchard in grass and other low vegetation immediately beat apple trees.	Paquin et al. 2010; Jäger, 2002; Urones, 1995; Ferrandez et al. 2006; Deltshev, 2004; Dorris, 1985; Crawford et al. 1995; West et al. 1988; Dondale et al. 1994; Cokendolpher, 1978
Theridion	varians	Hahn, 1833	minor	Introduced in Canada. Found in natural ecosystems (Outside)	Paquin et al. 2010; Jäger, 2002; Urones, 1995; Ferrandez et al. 2006; Deltshev, 2004; Dorris, 1989; Paquin personal comunication 2014
Theridula	opulenta	Walckenaer, 1842	minor	Introduced in Canada (cosmopolitan). This species is primarily south-eastern but there are scattered records from Utah and Oregon. They have been found in fields, bushes, and low vegetation forests. The web is reduced to a sparse tangle under a leaf. This species has occasionally been found together in the same areas as *Theridula emertoni*. The adults have sometimes been found together in one web. The female remains in her web with a small white egg case until the young emerge. Found in the South of France, Corcega, and Europe, Japan and Madagascar.	Paquin et al. 2010; Jäger, 2002; Urones, 1995; Ferrandez et al. 2006; Deltshev, 2004; Muma, 1975; Melic, 2000; Levi, 1954; Paquin personal comunication, 2014
Trachyzelotes	barbatus	L. Koch, 1866	minor	Mediterranean to Central Asia, USA (California).Found in a natural ecosystem (coastal sage scrub) but they haven't had a major impact. Its known distribution is Mediterranean to Central Asia, USA. New to Lesbos, but previously recorded in continental Greece and Crete.	Paquin et al. 2010; Jäger, 2002; Urones, 1995; Ferrandez et al. 2006; Deltshev, 2004; Dorris, 1991; Burger, 2001; Crespo and Mendes, 2010; Bosmans, 2011

Trachyzelotes	lyonneti	Audouin, 1826	minor	Mediterranean to Central Asia, USA, Brazil, Peru. The records scattered across the US from California to Illinois. It has been recorded from a wide variety of habitats, including suburban yards and inside buildings. This species hides under rocks in the daytime. Also introduced into Brazil and Peru. It is native of the Mediterranean region. Its been recorded in Ash Meadows National Wildlife Refuge.	Paquin et al. 2010; Jäger, 2002; Urones, 1995; Ferrandez et al. 2006; Deltshev, 2004; Dorris, 1992; Beatty, 2002; Oraze et al. 1988; Bowen et al. 2004; Crews and Stevens, 2009
Trochosa	ruricola	De Geer, 1778	minor	It was discovered in Cape Cod, Massachusetts, which outnumbered the native *T. terricola* in pitfall trap samples by a ratio somewhat greater than 2:1. It was also found in Canada, and on 1999 in Lake County, Illinois, where *T. terricola* outnumbered the non-native *T. ruricola* by a factor of approximately 2.5:1.	Paquin et al. 2010; Jäger, 2002; Urones, 1995; Ferrandez et al. 2006; Deltshev, 2004; Dorris, 1993
Urozelotes	rusticus	L. Koch, 1872	omajor	In coastal sage scrub, the non-native *Urozelotes rusticus* (Koch) seems to be involved in the competitive displacement of the native *Drassyllus insularis* (Banks), which is absent in the sites with a highest number of the invasive species (Burger et al., 2001). Is considered both a synanthropic and cosmopolitan species that has been found in very diverse ecosystems, such as rice fields in Sacramento Valley (California) and the Black Rock forest a nature reserve and research facility in Orange County (New York) (Platnick and Song, 1986; Oraze et al., 1988; Ovtcharenko et al., 2014).	Paquin et al. 2010; Jäger, 2002; Urones, 1995; Ferrandez et al. 2006; Deltshev, 2004; Dorris, 1994
Zelotes	nilicola	O. Pickard-Cambridge, 1874	minor	Mediterranean, Canary Is., USA (CA, AZ). It's found distribution: Egypt, Tunisia, Canary Islands, Corsica, Giglio Island close to Italy, Greece, Cyprus, Israel - new record, United States: Southern California, Arizona. It has been found in a natural ecosystem (coastal sage scrub) but they haven't had a major impact. Has been collected at many localities in southern California and adjacent Arizona since 1955, often in buildings, orchards, and agricultural fields.	Levy, 1998; Burger et al. 2001; Crews and Stevens, 2009; Platnick and Murphy, 1998; Platnick and Shadab, 1983; Bolger et al. 2008
Zodarion	rubidum	Simon, 1914	minor	Introduced in Canada. It also has been found in Pennsylvania, Ohio, Quebec, Colorado, and British Columbia. During the day these spiders hide under rocks in a small silk-lined chamber that is covered with sand. If disturbed during the day, they run rapidly and hide. At night they emerge to hunt ants. They have often been captured in pitfall traps. According to Paula Cushing and Richard Santagelo (2002), these little spiders eat exclusively ants.	Cushing and Santangelo, 2002; Pekar, 2004; Pekar, 2005

Zygiella	atrica	C. L. Koch, 1845	minor	Europe, Asia, North America (NF-NY, BC).It is locally abundant in New England, Nova Scotia, and southern Ontario; also Vancouver, British Columbia. In north-eastern NA, it often build its orb web near the ocean. It is said to prefer trees and shrubs for snare situations. The webs are incomplete as in typical species of the group. It was introduced into North America (Massachusetts), apparently from Europe, by 1885 and was abundant o the northern Massachusetts seacoast by 1909. It is now well-established, especially along the coast, from Newfoundland to Long Island, New York.	Spiller, 1992; Townley et al. 2012
Zygiella	x-notata	Clerck, 1757	minor	Europe, Asia, North America (ME-VA, BC-CA), South America (temperate), New Zealand. It was known to occur in NA well before the turn of the century. By 1911 it was reported to become abundant all over Cape Cod and the south shore of Massachusetts and Rhode Island. In New England is a house spider, on the west coast of NA, where is especially abundant, it lives on shrubs and trees, and rock cliffs and dirt banks along streams. It is a common orb spider in coastal areas of California. Newly recorded from japan, the known distributional range of the species includes Europe and China, and North (Pacific and Atlantic coasts) and South America (temperate) possibly as the secondary introduction. Under natural conditions, prey and conspecifics are present simultaneously, and commonly found on human constructions (fences or window frames)	Spiller, 1992; Tanikawa, 2004; Thévenard et al. 2004

Table A.1.4 Non-native spiders established in New Zealand natural ecosystems.

Genus	Species	species author	Impact level	Details	References
Anzacia	*gemmea*	Dalmas, 1917	minor	New Zealand, Australia (Phillip Island). Present in New Zealand in agrosystems in North Island of New Zealand. Also found in Philip Island. Is basically and Australian genus, introduced in New Zealand. Is also present in the pastures in the Waikato, in Kaikoura. One of the species identified as characteristic of the later stage in the post-burn succession (defined as a generalist species), abundant in burned areas (native grassland).	Topping and Lovei, 1997; Ovtsharenko and Platnick, 1995; Clark et al. 2004; Zakharov and Ovtcharenko, 2011; Malumbres-Olarte et al. 2013
Arachnura	*feredayi*	L. Koch, 1872	minor	Australia, Tasmania, New Zealand. Found in Canterbury, Tawhiti Rahi, Poor Knights. Also known as *Epeira feredayi*, the Punakaiki coastal restoration	Dondale, 1966; Hickman, 1925; Court, 1982; Gibbs, 1982; Bowie et al. 2012
Araeoncus	*humilis*	Blackwall, 1841	minor	Palearctic, New Zealand. Also known as *Walckenaera humilis*. Found in field-margins and pastures in Canterbury. Found in native grassland on later stage in the post-burn succession (generalist species).	McLachlan and Wratten, 2003; Malumbres-Olarte et al. 2013; Malumbres-Olarte et al. 2014; Blick et al. 2004; Tanasevitch, 2011
Argiope	*protensa*	L. Koch, 1872	minor	New Guinea, Australia, New Caledonia, New Zealand. Found in the Cavalli Islands (Northland), Whangaokena (east Island).	Roberts, 1979; Gibb et al. 2014; Chrysanthus, 1971; Gibbs, 1982; Hutcheson, 2000; Hickman, 1944; Vink personal comunication, 2014
Argoctenus	*aureus*	Hogg, 1911	minor	Australia, New Zealand, and New Caledonia.	Raven and Stumkat, 2003; Vink personal comunication, 2014
Argoctenus	*sp.*	Simon	minor	Australia, New Zealand. It was previously thought to be introduced and naturalised, now considered native.	Langlands, 2010; Sirvid et al. 2012; Langlands et al. 2012; Brennan et al. 2006; Bosselaers and Jocqué, 2013; Austin, 1985; Vink personal comunication, 2014

Argyrodes	*antipodianus*	O. Pickard-Cambridge, 1880	minor	Australia, New Caledonia, New Zealand. In Queensland (coastal regions of Australia), referred as a host specialist. In New Zealand *A. antipodianus* specialized on a single host species, *Eriophora pustulosa*, in whose webs it foraged most efficiently.	Grostal and Walter, 1999; Platnick, 1993; Grostal and Walter, 1997; Vink personal comunication, 2014
Australomimetus	*aurioculatus*	Hickman, 1929	minor	Australia, New Zealand. Originally described with no other locality than Tasmania. However, the species shows a wide distributional range and new records are established for Western Australia, New south Wales, Victoria and southern Queensland. The species seems to be habitat generalist.	Framenau et al. 2011; Framenau, 2010; Rendon et al. 2015;
Australomimetus	*robustus*	Heimer, 1986	minor	Queensland, NSW, New Zealand	Harms and Harvey, 2009; Harms and Harvey, 2009; Vink personal comunication, 2014
Backobourkia	*brounii*	Urquhart, 1885	minor	Australia, New Zealand. Found in Christchurch suggest the New Zealand population of *B. brounii* originated from eastern Australia. It may have ballooned to New Zealand as dispersal on a standard silk. Its known habitat preferences are open to closed sclerophyll forests but also parklands and gardens, occasionally found in grassland.	Harms and Harvey, 2009; Vink personal comunication, 2014
Badumna	*insignis*	L. Koch, 1872	minor	Australia, Japan, New Zealand. It is a necrotising spider found in Australia. It is typically widespread in the inland arid regions of Australia, but has been introduced into urban areas where it has become established in human habitations. It was observed during the night and during the day in trials using two types of prey, blowflies (*Lucilia cuprina*) and cockroaches (Blatta sp.). Associated with necrosis, frequently found in and around the Australian home. Observed in Canterbury (New Zealand) in nature reserves (Travis Swamp). In natural situations B. insignis builds its web under the shelter of logs, loose bark of trees rocks, cliffs and stones, preferring dry positions. However, its opportunistic nature has allowed it to take advantage of areas settled by humans, where it is quite common around houses, sheds, window-sills, under eaves and rafters, boxes and outdoor furniture.	Framenau et al. 2010; Kean et al. 2012; Vink personal comunicatio, 2014
Badumna	*longinqua*	L. Koch, 1867	minor	Eastern Australia, New Zealand, USA, Uruguay, and Germany. Later introduced to New Zealand, Japan and the New World. It can be found associated with tree trunks, rock walls and is very common in synantropic habitats, such as window frames, wall crevices, inside or outside houses, and in urban parks. In USA this species has been reported from rural woodlands to beachfront boulders and recently observed in vineyard plantations (California and Oregon). It can produce necrotic lesions	Young and Pincus, 2001; Henderson and Elgar, 1999; Lui et al. 2005; Bowie et al. 2006; Jackson, 1986; Hose et al. 2002; Clemente et al. 2005

				of the skin (controversial). It wasn't find on the nature by Jackson, 2002. In Argentina competition with the native *Metaltella simoni* has been observed. Found on Mokoia Island (lake Rotorua), but also in pastures or shelterbelts.	
Bianor	*maculatus*	Keyserling, 1883	minor	Australia, New Zealand, New Caledonia, Samoa, Vietnam. Considered an Australian species widely distributed	Jackson and Li, 2001; Jackson, 2002; Pompozzi et al. 2013; Meads and Fitzgerald, 2001; McLachland, 2000
Celaenia	*atkinsoni*	O. Pickard-Cambridge, 1879	minor	Australia, Tasmania, New Zealand	Peng and Li, 2003; Logunov, 2009; Vink personal comunication, 2014; Patoleta and Zabka, 1999; Platnick, 1993
Cheiracanthium	*stratioticum*	L. Koch, 1873	minor	New Zealand, Tasmania. It has been found in Christchurch, cohabiting with other individuals. Toxic bites have been reported in the country. The eggs are found in the rolled-up leaves of *P. tenax*.	Hickman, 1970; Vink personal comunication, 2014
Cryptachaea	*blattea*	Urquhart, 1886	minor	New Zealand, Belgium, USA (CA), Azores, Madeira, St Helena, Chile. Found associated with field margins on New Zealand farmland, also in burned tussock grasslands.	Jackson, 1986; Papini, 2012; Vink et al. 2011
Cryptachaea	*veruculata*	Urquhart, 1886	minor	Australia, New Zealand, England, Belgium. Also known as *Theridion calyciferum* Urquhart, 1886 from New Zealand and Achaearanea extrilida (Keyserling, 1890) from Australia are placed in synonym under C. veruculata.	Sirvid et al. 2012; Smith et al. 2012; Bowie et al. 2014; Malumbres-Olarte et al. 2014; Vink et al. 2009
Cyclosa	*trilobata*	Urquhart, 1885	minor	Australia, Tasmania, New Zealand. Found on Mokoia Island, Lake Rotorua; Tawhiti Rahi, Poor Kinghts Islands (on open scrub on site of burn);	Smith et al. 2012; Eberhard et al. 2014; Vink personal comunication, 2014
Diplocephalus	*cristatus*	Blackwall, 1833	major	This species is widespread in New Zealand, especially in agroecosystems and human-modified areas, and it has multiple records in natural ecosystems, such as native tussock grasslands at Deep Stream (East Otago Plateau), modified native shrub land at Brookdale Conservation Covenant (Rock and Pillar Range, Otago), and in native forest at Hinewai Reserve. Moreover, it shares a similar niche with several tiny endemic species, which may have been displaced (Vink pers. obs.), and it is the dominant species in native burned tussock grassland.	Meads and Fitzgerald, 2001; Court, 1982; Gibbs, 1982; Ward et al., 1999; Derraik et al., 2001; Derraik et al., 2002; Derraik et al., 2005; Phillips et al., 2008: Malumbres-Olate et al., 2013: Vink personal

					Comunication, 2014; Malumbres-Olate et al., 2014
Erigone	*prominens*	Bösenberg & Strand, 1906	minor	Cameroon to Japan, Vietnam, New Zealand. Also known as *Erigone riparia*. Found in carrot fields, field-margin and pasture spiders, arable crops and grasses, Canterbury.	Malumbres-Olate et al. 2014; Malumbres-Olate et al. 2013; Derraik et al 2001; Derraik et al. 2002; Derraik et al. 2005; Ward et al. 1999
Erigone	*wiltoni*	Locket 1973	minor	Comoro Is., New Zealand. Considered generalist. Associated with plots where burning occurred in NZ, on the later stage in the post-burn succession. Also found in habitats with reduced disturbance. Also found in carrot fields in Canterbury. Also found in field-margin and pastures in Canterbury. Found on cultivation in pastures in the Waikato. And in arable crops and grasses in Canterbury.	Locket, 1973; Sivasubramaniam et al. 1997; McLachland and Wratten, 2003; Vink et al. 2004; Tu and Li, 2004; McLachlan, 2000; Clark et al.2004 ; Vink personal comunication, 2014
Eriophora	*decorosa*	Urquhart, 1894	minor	New Zealand, Australia	Locket, 1973; Malumbres-Olarte et al. 2013; McLachlan, 2000; Topping and Lovei, 1997; Sivasubramaniam et al. 1997; McLachlan and Wratten, 2003; Clark et al. 2004; Vink et al. 2004; Vink personal comunication, 2014
Eriophora	*pustulosa*	Walckenaer, 1842	minor	Australia, Tasmania, New Zealand; Difficult to find in the wild, often collected in gardens (NZ). Characteristically feeds on one housefly and leaves the other flies wrapped and uneaten in its web. Host of *A. antipodiana*. Found on a modified native shrubland, Brookdale Covenant, Rock and Pillar Range (Otago). Found in Quail Island and Travis Swamp.	Paquin et al. 2008; Framenau et al. 2010; Vink personal comunication, 2014
Helpis	*minitabunda*	L. Koch, 1880	minor	New Guinea, Eastern Australia, New Zealand. In NZ its nest or web site is in buildings	Toft and Rees, 1998; Whitehouse, 1997; Whitehouse and Jackson, 1994; Derraik et al. 2001;

					Jackson, 1992; Bowie et al. 2006; Hodge et al. 2007
Hemicloea	*rogenhoferi*	L. Koch, 1875	minor	Queensland, New South Wales, New Zealand; Also found in Quail Island.	Jackson, 1987; Hallas and Jackson, 1986; Taylor, 1995; Vink personal comunication, 2014
Hogna	*crispipes*	L. Koch, 1877	minor	New Guinea, New Hebrides, Polynesia, New Zealand. Distributed in the Pacific islands (incl. New Zealand and Hawaii). Found in Brassica crops in South Australia. Is found on mainland Australia and offshore islands and reefs in the East and West of Australia, as well as in New Zealand and on several Pacific islands.	Denholm, 2003; Bowie et al. 2006; Hodge et al. 2007
Holoplatys	*appressus*	Powell, 1893	minor	New Zealand.	Sirvid et al. 2012; Hosseini et al. 2007; Murphy et al. 2006; Gonzalez, 2012; Framenau et al. 2006; Vink personal comunication, 2014
Laperousea	*blattifera*	Urquhart, 1887	minor	Australia, New Zealand. Found in Te Paki Ecological District (Northland, New Zealand) it is rarely caught in pitfall traps but are common and widespread.	Vink personal communication, 2014
Latrodectus	*hasseltii*	Thorell, 1870	major	Southeast Asia to Australia, New Zealand. The studies suggested that the spiders could become dispersed throughout New Zealand by wind, but that their survivorship would depend largely on the availability of arid habitats, as well as the suitability of summer temperatures for breeding and appropriate conditions for overwintering. At least 36 individuals *of Latrodectus hasseltii* were intercepted in New Zealand in 1966-82, all from goods being brought into the country from Australia. Venomous spider. It was found feeding on several native arthropods classified as 'range restricted' and 'nationally endangered' (*Prondontria modesta* and *Mimopeus* sp., and *Prodontria lewisii*, respectively). *Latrodectus hasseltii* can potentially displace the endemic L. katipo and even though it has not been recorded from sand dunes, there is genetic evidence of hybridization. Moreover, successfully cross-breeding experiments have been conducted, *indicating L. hasseltii* could bring *L. katipo* to extinction via hybridization.	Vink et al., 2008; Ball and Fitzgerald, 2011; Vink et al., 2011: Vink personal comunication, 2014; Bryan et al., 2015

Leucauge	*dromedaria*	Thorell, 1881	minor	Australia, New Zealand. Found in the Mokoia Island, Lake Rotorua	Forster, 1984; Froster, 1992; Garb et al. 2004; Vink et al. 2011; Vink et al. 2008; Griffiths, 2001; Manju and Kumar, 2001
Mermessus	*fradeorum*	Berland, 1932	minor	North America, Azores, South Africa, New Zealand. A common web-building spider in North America grasslands and agricultural fields.	Meads and Fitzgerald, 2001; Court, 1982
Microctenonyx	*subitaneus*	O. Pickard-Cambridge, 1875	minor	Holarctic, Chile, NZ. Found an adjacent fenced off *Pinus radiata* shelterbelt in Canterbury (NZ). Is endemic to the Holarctic, it is known from other regions including Africa and New Zealand.	Welch et al. 2013; Vink personal comunication, 2014
Nanometa	*gentilis*	Simon, 1908	minor	Australia, New Zealand	McLachlan, 2000; Brennan, 2004; McLachlan and Wratten, 2003; Blick et al. 2004
Nephila	*edulis*	Labillardière, 1799	minor	Australia, New Caledonia, New Zealand	Vink personal comunication, 2014
Novakiella	*trituberculosa*	Roewer, 1942	minor	Australia, New Zealand	Platnick, 1993: Vink personal comunication, 2014
Ostearius	*melanopygius*	O. Pickard-Cambridge, 1879	minor	Cosmopolitan. Countries AT, BE, BG, CH,CZ, DE, DK, ES, FR, FI, GB, IT, NL, PT, PL, RO, SE, SK. Found in arable crops and grasses in Canterbury, New Zealand	Vink personal comunication, 2014
Oxyopes	*gracilipes*	White, 1849	minor	Australia, Tasmania, New Zealand. Its known distribution is TH, ND, AK, CL, WO, BP, GB, TO, TK, HB, RI, WI, WN WA, NN, KA, BR, NC, MC, WD, MK, OL, CO, DN. Usually found on low shrubs, tall grass and tussock. Found in field-margins and pastures in Canterbury.	Nentwig and Kobelt, 2010; Vink et al. 2004; Vink personal comunication, 2014
Sidymella	*longipes*	L. Koch, 1874	minor	Australia, New Zealand. It was reported for the first time in Sirvid et al. (2010). Museum collection records indicate that it has been present in the upper North Island of several decades	Vink and Sirvid, 1998; McLachland and Wratten, 2003; Whyte, 2011
Steatoda	*capensis*	Hann, 1990	major	An invasive species that may be displacing the endemic *Latrodectus katipo* Powell, which is classified as 'declining' due to habitat destruction and modification. *Latrodectus katipo* inhabits New Zealand's coastal dune systems, but seems to have been permanently displaced along the Otaki-Wangaui coast. Even though evidence of competition has not been found, *S. capensis* is likely to	Hann, 1990; Hann, 1994; Costall and Death, 2009; Costall and Death, 2010; Sirvid et al. 2012; Sirvid et al. 2013; Vink personal comunication, 2014;

				have an advantage because of its ability to reproduce year-round and its wider habitat tolerance.	Hetherington and Wilson, 2014
Supunna	*picta*	L. Koch, 1873	minor	Queensland, New Zealand. Is a recent introduction from Australia, now found commonly in New Zealand around houses and in open country with short grass cover. Also found in burned New Zealand tussock grasslands. First discovered in Auckland during the 1940s and has now extended its range south to become common in the Bay of Plenty. It has recently become established in Canterbury. It is commonly found under driftwood or leaf foliage on the sand-dunes and amongst the wood scattered along riverbanks.	Garb et al. 2004; Hann, 1990; Costall and Death, 2010; Coastall and Death, 2009; Hetherington and Wilson, 2014; Hann, 1994; Atakuziev et al. 2014
Tenuiphantes	*tenuis*	Blackwall, 1852	minor	Europe, North Africa (elsewhere, introduced: Canary Islands, Canada (British Columbia, Newfoundland), USA (Hawaii, Washington, Oregon, and Massachusetts), Chile and Argentina). On a sampling in arable crops and grasses sites in Canterbury it was the most abundant species. It was also reported as the most abundant spider species in North Island pasture and Canterbury pasture. It is also common in agroecosystems in England and other European countries. It is considered a potential biological control agent for cereal pests. Probably introduced to NZ in colonial times, it also occurs in disturbed native forest and pine plantations. Is not known on what it feeds, although it has been really reported feeding on *L. bonariensis*. IT is also one of the first colonizers of burned areas.	Jackson and Poulsen, 1990; Malumbres-Olarte et al. 2014; Gibbs, 1982
Tetragnatha	*nitens*	Audouin, 1826	minor	Cosmotropical. This is a species with a very wide distribution, from the Mediterranean to several of the Pacific island. This species is widespread throughout the Mediterranean area (including southernmost France), almost all of African to the Cape, Australia, New Zealand, and the Chatham islands, and Polynesia. Found on Mokoia Island, Lake Rotorua.	Vink et al. 2004; Mclachlan and Wratten, 2003; Vink and Kean, 2013; Clark et al. 2004; Malumbres-Olarte et al. 2013; Bowie et al. 2014; Malumbres-Olarte et al. 2014; Blick et al. 2004; Brockerhoff et al. 2009
Toxopsoides	*huttoni*	Forster & Wilton, 1973	minor	Eastern Australia, New Zealand. Its distribution in NZ in North Island, Waitetoko, near Lake Taupo. However, it has a limited distribution, could be an accidental introduction from Australia, where it is widespread in south-eastern states.	Marples, 1975; Sirvid et al. 2012; Gillespie, 2003; Berland, 1942; Vink personal comunication, 2014; Deltshev et al. 2013

Venatrix	*konei*	Berland, 1924	minor	Australia, Lord Howe Is., New Zealand. Recently recorded from New Caledonia	Smith, 2013; Vink personal comunication, 2014

A.2 Contingency table with the number and proportion of species of each biogeographic origin per level of impact (biological control agents not included)

Taxon	Eozone	Region	Impact				
			None	Minor	Omajor	Major	Totals
Beetles	Afrotropical (AFRT)	NthAm	**1**/1 = 100%	**0**/1 = 0%	**0**/1 = 0%	**0**/1 = 0%	**1**/ 180 = 0.6%
		NZ	**1**/2 = 50%	**1**/2 = 50%	**0**/2 = 0%	**0**/2 = 0%	**2**/62 = 3%
	Australasia (AUST)	NthAm	**5**/7 = 72%	**1**/7 = 14%	**1**/7 = 14%	**0**/7 = 0%	**7**/180 = 4%
		NZ	**20**/26 = 77%	**6**/26 = 23%	**0**/26 = 0%	**0**/26 = 0%	**26**/62 = 42%
	Cosmopolitan (COSM)	NthAm	**1**/2 = 50%	**1**/2 = 50%	**0**/2 = 0%	**0**/2 = 0%	**2**/180 = 1%
		NZ	**0**/0 = 0%	**0**/0 = 0%	**0**/0 = 0%	**0**/0 = 0%	**0**/62 = 0%
	Indomalayan (INDM)	NthAm	**6**/9 = 67%	**2**/9 = 22%	**1**/9 = 11%	**0**/9 = 0%	**9**/180 = 5%
		NZ	**2**/2 = 100%	**0**/2 = 0%	**0**/2 = 0%	**0**/2 = 0%	**2**/62 = 3%
	Nearctic (NEAR)	NthAm	**2**/3 = 67%	**0**/3 = 0%	**1**/3 = 33%	**0**/3 = 0%	**3**/180 = 2%
		NZ	**1**/1 = 100%	**0**/1 = 0%	**0**/1 = 0%	**0**/1 = 0%	**1**/62 = 2%
	Neotropical (NEOT)	NthAm	**8**/17 = 47%	**7**/17 = 41%	**1**/17 = 6%	**1**/17 = 6%	**17**/180 = 9%
		NZ	**9**/11 = 82%	**2**/11 = 18%	**2**/11 = 0%	**2**/11 = 0%	**11**/62 = 18%
	Palearctic (PALE)	NthAm	**70**/148 = 47%	**43**/148 = 29%	**12**/148 = 8%	**6**/148 = 4%	**148**/180 = 82%
		NZ	**17**/19 = 89%	**2**/19 = 10%	**0**/19 = 0%	**0**/19 = 0%	**19**/62 = 31%
	Not known	NthAm	**7**/10 = 70%	**2**/10 = 20%	**1**/10 = 10%	**0**/10 = 0%	**0**/180 = 0%
		NZ	**1**/1 = 100%	**0**/1 = 0%	**0**/1 = 0%	**0**/1 = 0%	**0**/62 = 0%
Spiders	Afrotropical (AFRT)	NthAm	**1**/2 = 50%	**1**/2 = 50%	**0**/2 = 0%	**0**/2 = 0%	**2**/111 = 2%
		NZ	**0**/0 = 0%	**0**/0 = 0%	**0**/0 = 0%	**0**/0 = 0%	**0**/70 = 0%
	Australasia (AUST)	NthAm	**0**/1 = 0%	**1**/1 = 100%	**0**/1 = 0%	**0**/1 = 0%	**1**/111 = 1%
		NZ	**13**/46 = 28%	**32**/46 = 70%	**0**/46 = 0%	**1**/46 = 2%	**46**/70 = 66%
	Cosmopolitan (COSM)	NthAm	**8**/17 = 47%	**7**/17 = 41%	**2**/17 = 12%	**0**/17 = 0%	**17**/111 = 15%
		NZ	**0**/0 = 0%	**1**/0 = 100%	**0**/0 = 0%	**0**/0 = 0%	**0**/70 = 0%
	Holarctic (HOLA)	NthAm	**3**/5 = 60%	**2**/5 = 40%	**0**/5 = 0%	**0**/0 = 0%	**0**/111 = 0%
		NZ	**1**/3 = 33%	**1**/3 = 33%	**0**/3 = 0%	**1**/3 = 33%	**3**/70 = 4%
	Indomalayan (INDM)	NthAm	**0**/0 = 0%	**0**/0 = 0%	**0**/0 = 0%	**0**/0 = 0%	**0**/111 = 0%
		NZ	**1**/1 = 100%	**0**/1 = 0%	**0**/1 = 0%	**0**/1 = 0%	**1**/70 = 1%
	Nearctic (NEAR)	NthAm	**0**/0 = 0%	**0**/0 = 0%	**0**/0 = 0%	**0**/0 = 0%	**0**/111 = 0%
		NZ	**1**/2 = 50%	**1**/2 = 50%	**0**/2 = 0%	**0**/2 = 0%	**2**/70 = 3%
	Neotropical (NEOT)	NthAm	**5**/9 = 56%	**4**/9 = 44%	**0**/9 = 0%	**0**/9 = 0%	**9**/111 = 8%
		NZ	**1**/2 = 50%	**0**/2 = 0%	**0**/2 = 0%	**1**/2 = 50%	**2**/70 = 3%
	Palearctic (PALE)	NthAm	**39**/66 = 59%	**25**/66 = 38%	**2**/66 = 3%	**0**/66 = 0%	**66**/111 = 59%
		NZ	**7**/11 = 63%	**4**/11 = 36%	**0**/11 = 0%	**0**/11 = 0%	**11**/70 = 16%
	Pantropical (PANT)	NthAm	**3**/3 = 100%	**0**/3 = 0%	**0**/3 = 0%	**0**/3 = 0%	**3**/111 = 3%
		NZ	**1**/2 = 50%	**1**/2 = 50%	**0**/2 = 0%	**0**/2 = 0%	**2**/70 = 3%
	Not known	NthAm	**7**/8 = 87%	**1**/8 = 13%	**0**/8 = 0%	**0**/8 = 0%	**8**/111 = 7%
		NZ	**0**/1 = 0%	**1**/1 = 0%	**0**/1 = 0%	**0**/1 = 0%	**1**/70 = 1%

Appendix B

Can measures of floristic composition improve predictions of non-native pest establishment success based on climate matching alone?

B.1 Table of variables selected from the GLMM models and the GLM individual species models

	Model name	Target region	Variables selected
General Linear Mixed Model (GLMM)	'native/exotic'	Kansas	EJ, NJ, PDE, PDN, EJ:NJ, EJ:PDE, NJ:PDN, NJ:PDE, PDE:PDN
		Virginia	EJ, NJ, PDE, PDN, EJ:NJ, EJ:PDE, EJ:PDN, NJ:PDE, NJ:PDN
		New Zealand	EJ, NJ, PDE, PDN, EJ:NJ, EJ:PDE, EJ:PDN, NJ:PDE, NJ:PDN, PDE:PDN
	'all plants'	Kansas	EJ, PD, GJ:PD
		Virginia	EJ, PD, GJ:PD
		New Zealand	EJ, PD, GJ:PD
	'native/exotic & climate'	Kansas	CMI, EJ, NJ, PDE, PDN, CMI:PDN, EJ:NJ, EJ:PDE, EJ:PDN, NJ:PDE, NJ:PDN, PDE:PDN
		Virginia	CMI, EJ, NJ, PDE, PDN, CMI:EJ, CMI:NJ, CMI:PDE, EJ:PDE, NJ:PDN
		New Zealand	CMI, EJ, NJ, PDE, PDN, CMI:EJ, CMI:NJ, CMI:PDE, CMI:PDN, EJ:NJ, EJ:PDN
	'all plants & climate'	Kansas	CMI, GJ, PD, CMI:GJ, GJ:PD, CMI:GJ:PD
		Virginia	CMI, GJ, PD, CMI:GJ, GJ:PD, CMI:GJ:PD
		New Zealand	CMI, GJ, PD, CMI:GJ, GJ:PD, CMI:GJ:PD
Individual species Generalized Linear Models (GLM)	'native/exotic'	Kansas	EJ, NJ, PDE, PDN, EJ:PDE, NJ:PDN
		Virginia	EJ, NJ, PDE, PDN, EJ:PDE, NJ:PDN
		New Zealand	EJ, NJ, PDE, PDN, EJ:PDE, NJ:PDN
	'all plants'	Kansas	GJ, PD, GJ:PD
		Virginia	GJ, PD, GJ:PD
		New Zealand	GJ, PD, GJ:PD
	'native/exotic & climate'	Kansas	CMI, GJ, PD, CMI:GJ
		Virginia	CMI, GJ, PD, CMI:GJ
		New Zealand	CMI, GJ, PD, CMI:GJ
	'all plants & climate'	Kansas	CMI, EJ, NJ, PDE, NPD, EJ:NJ, NJ:PDN
		Virginia	CMI, EJ, NJ, PDE, NPD, EJ:NJ, NJ:PDN
		New Zealand	CMI, EJ, NJ, PDE, NPD, EJ:NJ, NJ:PDN

Of all the potential models fitted, just one was chosen for each set ('native/exotic', 'all plants', 'native/exotic & climate' and 'all plants & climate') across all target regions and species for both GLMMs and GLMs. The chosen model had on average (for regions and species) the lowest AICc, and

therefore was the best approximating model according to the goodness of fit. For the GLMs, sets of models with lower complexity, such as 'all plants' and 'all plants & climate', had similar AICc across regions and species when the two-way interaction terms GJ:PD and CMI:GJ respectively, were considered. However, the AICc were much more variable between models for 'native/exotic' and 'native/exotic & climate', and the final model chosen was not always the one with the lowest AICc for all species and regions. The reason was that models with the lowest AICc of each beetle species for the three target regions had different selections of two-way interaction terms.

B.2 Table of results of each of the GLM models for the three individual species in the selected regions

Target region	Species	Model	Variables	2.5%	97.5%	Deviance explained (%)
New Zealand	*Scolytus multistriatus*	'all plants & climate'	CMI	-1.31e+00	7.62	0.26
			GJ	-1.19e+01	35.68	0.11
			PD	8.39e-05	0.0002	16.09
			CMI:GJ	-4.26e+01	13.01	0.49
		'native/exotic & climate'	CMI	-6.96e-01	5.32	0.26
			EJ	-1.12e+01	8.57	0.67
			NJ	-1.48e+01	60.87	0
			PDE	-4.93e-04	0.0005	0.14
			PDN	1.59e-4	0.0004	17.53
			EJ:NJ	-1.16e+01	48.69	0.12
			NJ:PDN	-5.28e-03	-0.0005	2.55
	Otiorhynchus sulcatus	'all plants & climate'	CMI	-5.49e-01	8.38e+00	2.60
			GJ	-2.51e+01	2.84e+01	0.22
			PD	1.66e-05	9.28e-05	3.99
			CMI:GJ	-3.26e+01	2.59e+01	0.02
		'native/exotic & climate'	CMI	-6.80e-03	6.86	2.60
			EJ	-1.01e+01	17.89	1.73
			NJ	-1.58e+01	47.81	0.00
			PDE	-1.33e-03	0.0003	0.78
			PDN	2.90e-05	0.00002	3.22
			EJ:NJ	-1.96e+01	31.93	0.04
			NJ:PDN	-3.49e-03	0.0002	1.19
	Rhinocyllus conicus	'all plants & climate'	CMI	-1.12e+00	8.64	2.60
			GJ	-3.12e+01	29.07	0.30
			PD	3.67e-05	0.0001	8.29
			CMI:GJ	-3.29e+01	32.17	0.00
		'native/exotic & climate'	CMI	4.29e-01	7.53	2.60
			EJ	-1.29e+01	6.38	0.83
			NJ	-1.98e+01	56.23	0.03
			PDE	-3.28e-04	0.0005	0.01
			PDN	3.62e-05	0.0002	8.07
			EJ:NJ	-2.72e+01	27.44	0.00
			NJ:PDN	-3.26e-03	0.0008	0.81
Kansas	*Scolytus multistriatus*	'all plants & climate'	CMI	-2.49 e+01	-7.86e+00	36.94
			GJ	6.88e+00	2.95e+00	18.72
			PD	-5.96e+00	8.29e+01	0.13
			CMI:GJ	-9.15e+01	8.83e+00	0.78
		'native/exotic & climate'	CMI	7.85e+00	1.78e+01	36.94
			EJ	-1.96e+00	1.83e+01	8.55
			NJ	-2.50e+01	1.22e+01	2.54
			PDE	5.27e-05	6.66e-04	3.16
			PDN	-1.78e-04	2.77e-05	0.03
			EJ:NJ	-3.89e+01	1.80e-01	0.32
			NJ:PDN	-2.77e-04	2.54e-03	1.11
	Otiorhynchus sulcatus	'all plants & climate'	CMI	5.17e+00	1.49e+01	13.54
			GJ	1.19e+01	3.87e+01	3.84
			PD	-6.59e-05	2.37e-05	0.13
			CMI:GJ	-4.29e+1	-1.09e+01	4.06
		'native/exotic & climate'	CMI	1.27e+00	1.02e+01	13.54
			EJ	1.23+01	3.29e+01	5.86
			NJ	-1.68e+01	4.25e+00	1.49
			PDE	6.22e-04	1.55e-03	13.02
			PDN	-2.21e-04	-5.42e-05	4.59
			EJ:NJ	-2.77e+01	-8.65e+00	3.66
			NJ:PDN	-2.79e-04	7.41e-04	0.29
	Rhinocyllus conicus	'all plants & climate'	CMI	4.76e+00	2.091e+01	32.65
			GJ	-1.91e+01	2.37e+01	1.80
			PD	-6.03e-05	4.17e-05	0.05
			CMI:GJ	-2.68e+01	2.79e+01	0.00
		'native/exotic & climate'	CMI	9.69e+00	2.14e+01	32.65
			EJ	-8.44e+00	1.26e+01	0.52
			NJ	-2.94e+01	7.42e-01	0.05
			PDE	3.39e-04	1.05e-03	5.79

			PDN	-2.21e-04	-5.09e-05	2.62
			EJ:NJ	-1.71e+01	3.66e+01	0.08
			NJ:PDN	8.92e-06	1.32e-03	1.66
Virginia	*Scolytus multistriatus*	'all plants & climate'	CMI	8.55e+00	2.39e+01	37.63
			GJ	1.79e+01	6.49e+01	19.49
			PD	-3.90e-05	5.78e-05	0.001
			CMI:GJ	-6.82e+01	-8.18e+00	1.37
		'native/exotic & climate'	CMI	6.73e+00	1.37e+01	37.63
			EJ	-5.29e+00	1.22e+01	11.79
			NJ	-5.19e+01	1.11e+00	1.07
			PDE	-1.54e-04	3.40e-04	0.04
			PDN	-1.41e-04	-7.39e-06	0.28
			EJ:NJ	-1.37e+01	1.55e+02	0.93
			NJ:PDN	2.92e-05	1.90e-03	1.58
	Otiorhynchus sulcatus	'all plants & climate'	CMI	1.02e+01	2.01e+01	26.27
			GJ	1.63e+01	4.03e+01	1.13
			PD	-7.10e-05	1.22e-05	0.19
			CMI:GJ	-4.53e+01	-1.72e+01	6.09
		'native/exotic & climate'	CMI	3.96e+00	1.02e+01	26.27
			EJ	1.31e+01	2.88e+01	4.63
			NJ	-6.05e+00	3.77e+00	6.61
			PDE	-1.65e-04	2.58e-04	0.24
			PDN	-6.44e-05	5.69e-05	0.05
			EJ:NJ	-2.56e+01	-8.21e+00	2.85
			NJ:PDN	-2.65e-04	1.57e-04	0.07
	Rhinocyllus conicus	'all plants & climate'	CMI	7.45e+00	1.71e+01	23.43
			GJ	7.31e+01	3.72e+01	3.11
			PD	-2.95e-05	5.39e-05	0.27
			CMI:GJ	-4.06e+01	-1.25e+01	4.43
		'native/exotic & climate'	CMI	3.48e+00	9.26e+00	23.43
			EJ	5.66e-01	1.41e+01	2.80
			NJ	-1.12e+01	1.29e+00	1.42
			PDE	-6.26e-05	3.81e-04	0.79
			PDN	-4.79e-05	5.68e-05	0.57
			EGH:NJ	-1.35e+01	1.09e+01	0.003
			NJ:PDN	-5.61e-05	4.22e-04	0.84

CMI' = Composite Match Index; 'NJ' = Jaccard similarity index of native plants at genus level; 'EJ' = Jaccard similarity index of exotic plants at genus level; 'PDN = Phylogenetic diversity of native plants at genus level; 'PDE' = Phylogenetic diversity of exotic plants at genus level; 'GJ' = Jaccard similarity of all plants at genus level; 'PD'= Phylogenetic diversity of all plants at genus level.

B.3 Boxplots of the distribution of the different variables depending on the presence or absence of the non-native beelte species studied.

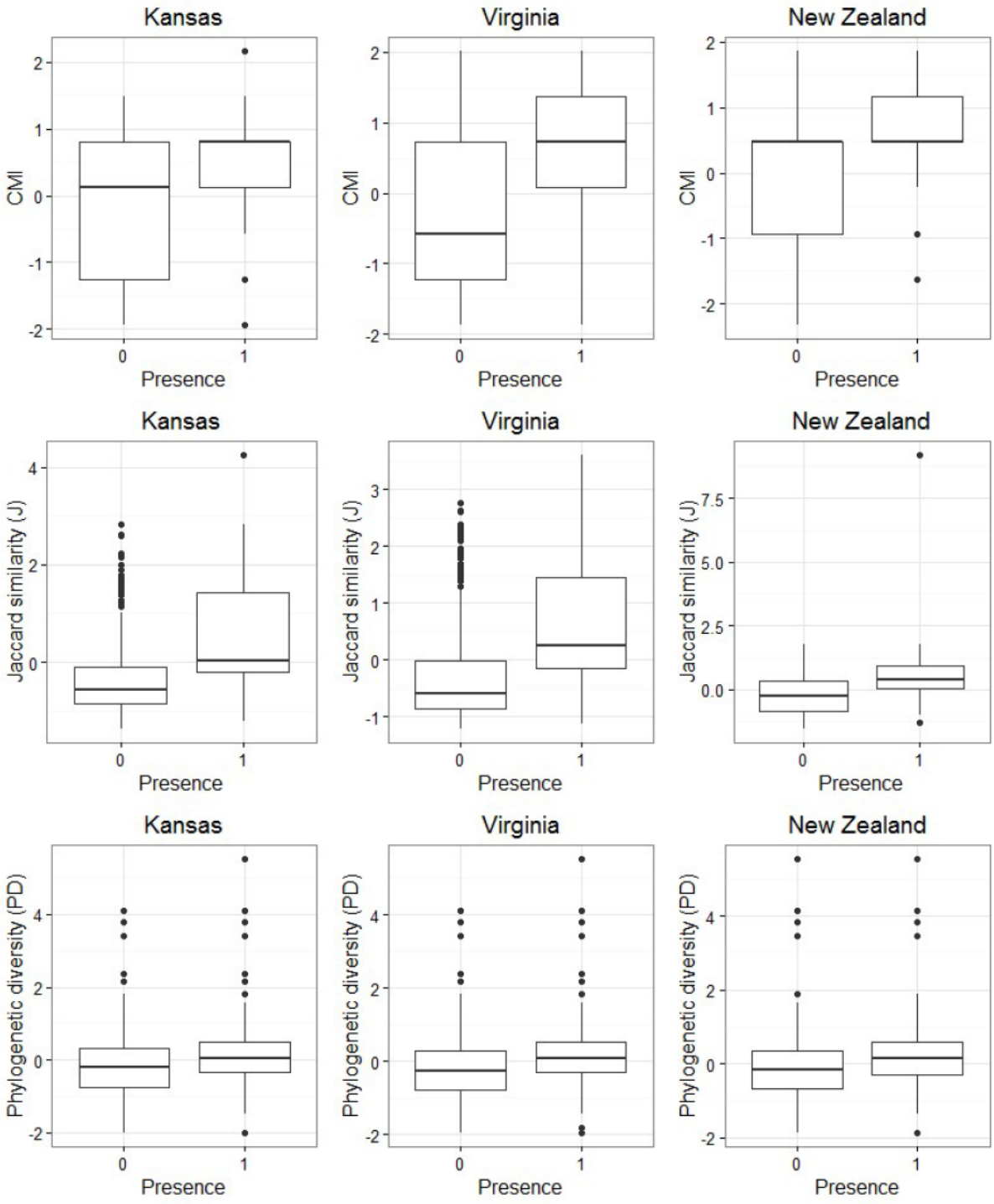


Figure B.3.1 Boxplots of the distribution of the climate matching index (CMI), Jaccard similarity of all plants (J) and phylogenetic diversity of all the plants (PD) depending on the presence or absence of the non-native beetle species studied.

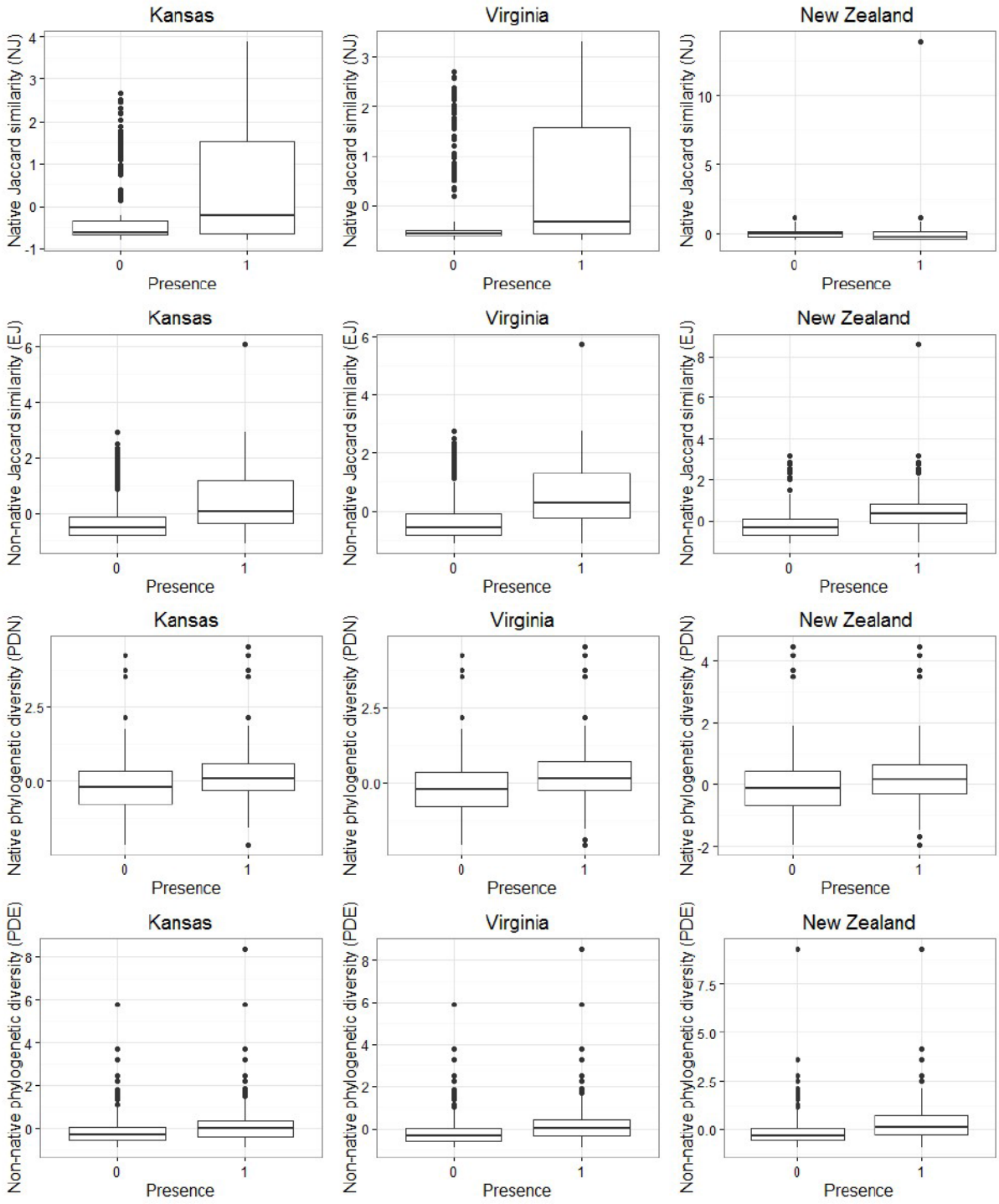


Figure B.3.1 Boxplots of the distribution of the Jaccard similarity of native (NJ) and non-native plants (EJ) and phylogenetic diversity of native (PDN) and non-native plants (PDE) depending on the presence or absence of the non-native beetle species studied.

Appendix C Phylogenetic signal as a predictor of host range of non-native invertebrate herbivores established in New Zealand and potential invaders

C.1 Table of coefficients of logistic regressions of host phylogenetic distance, number of known hosts and their interaction.

	Coefficients				95% confidence intervals			
Organisms class (n)	β_0	β_1	β_2	β_3	β_0	β_1	β_2	β_3
Adenophoera (38)	1.7315	-2.3884	0.0599	0.0177	1.7009 to 1.7606	-2.3992 to -2.3778	0.0551 to 0.0648	0.0157 to 0.0197
Arachnida (79)	2.3598	-2.7426	0.0907	-0.0204	2.3205 to 2.3990	-2.7579 to -2.7274	0.0833 to 0.0980	-0.0234 to -0.0175
Insecta (444)	2.6388	-3.3126	-0.0108	0.0220	2.6283 to 2.6494	-3.3169 to -3.3083	-0.0118 to -0.0097	0.02162 to 0.0224
Insecta order (n)	β_0	β_1	β_2	β_3	β_0	β_1	β_2	β_3
Coleoptera (79)	2.2564	-2.8934	0.1276	-0.0152	2.2310 to 2.5816	-2.9041 to 2.8826	0.1225 to 0.1327	-0.0174 to -0.0131
Diptera (29)	6.5713	-4.5512	0.1421	-0.0044	6.4713 to 6.6714	-4.5953 to -4.5072	0.1277 to 0.1565	-0.0105 to 0.0018
Hemiptera (231)	2.3179	-2.6738	2.3179	-2.6738	2.3028 to 2.3329	-2.6805 to -2.6671	2.3028 to 2.3329	-2.6805 to -2.6671
Hymenoptera (27)	5.2194	-4.3227	0.1167	-0.0199	5.1689 to 5.2699	-4.3469 to -4.2984	0.1079 to 0.1256	-0.0243 to -0.0157
Lepidoptera (61)	3.4816	-3.5305	0.0097	0.0354	3.4517 to 3.5115	-3.5438 to -3.5172	0.0068 to 0.0126	0.0342 to 0.0367
Thysanoptera (16)	3.0863	-2.3695	3.0863	-2.3695	3.0452 to 3.1273	-2.3882 to -2.3508	3.0452 to 3.1273	-2.3882 to -2.3508

*Coefficients of logistic regressions (median and 95% confidence intervals) of phylogenetic signal in host sharing with two independent variables and their interaction: Phylogenetic distance between source host genus and target host genus (coefficient β1); number of known hosts for the herbivore (coefficient β2); and their interaction (coefficient β3). The dependent variable was whether the target host genus was known to be susceptible (S) to a pest for the source host genus. The regression takes the form of logit(S) = β0 + β1 * log10(PD + 1) + β2*(Number of known hosts) + β3 * [(log10(PD + 1)) * (Number of known hosts)]. Only main effects, and not the interaction term, were included in the models presented in the main text.*

C.2 List of New Zealand native plants that might be threatened by Coleoptera species in the GPDD database

Rank number	Plant genus name	Num. NZ potential pests	Probability rank
1	Solanum	17	0.9546 – 0.1119
2	Apium	7	0.9546 – 0.3158
	Dacus	7	0.9546 – 0.3158
3	Ipomoea	5	0.9546
	Sicyos	5	0.9546
4	Rubus	4	0.9549
5	Linum sp.	1	0.9549
	Aristotelia	1	0.9549
	Nothofagus	1	0.9549
	Sophora	1	0.9549
	Dysoxylum	1	0.9549
	Hypericum	1	0.9549
	Lythrum	1	0.9549
6	Leptinella	4	0.3720 – 0.2230
	Cotula	4	0.3720 – 0.2230
	Celmisia	4	0.3720 – 0.2230
	Pachystegia	4	0.3720 – 0.2230
	Vittadinia	4	0.3720 – 0.2230
	Olearia	4	0.3720 – 0.2230
	Centipeda	4	0.3720 – 0.2230
7	Aciphylla	7	0.3157
8	Arthropodium	1	0.2751
	Cordyline	1	0.2751
9	Scleranthus	1	0.2599
10	Microseris	3	0.2536
11	Camichaelia	17	0.2356 – 0.1092
	Clianthus	17	0.2356 – 0.1092
	Swainsona	17	0.2356 – 0.1092
12	Micromeria	3	0.2197 – 0.1087
	Vitex	3	0.2197 – 0.1087
13	Gaultheria	3	0.2164
	Pernettya	3	0.2164
14	Parsonsia	3	0.2075
15	Rhopalostylis	8	0.2016
16	Arthropodium	1	0.1821
	Cordyline	1	0.1821
17	Discaria	4	0.1663 – 0.1039
18	Muehlenbeckia	5	0.1541
19	Anaphalioides	4	0.1518
	Craspedia	4	0.1518
	Leucoqenes	4	0.1518
	Ozothamnus	4	0.1518
	Pseudognaphalium	4	0.1518
	Raoulia	4	0.1518
20	Mazus	3	0.1412 – 0.1087
21	Tecomanthe	2	0.1412
22	Indigofera	27	0.1279
23	Beilschmiedia	7	0.1263
24	Kunzea	16	0.1183
	Lophomyrtus	16	0.1183
	Metrosideros	16	0.1183
25	Nestegis	4	0.1179
26	Urtica	2	0.1005
	Viola	2	0.1005

Table clarifications: being 'Num. NZ potential hosts' the number of plants that according to the phylogenetic distance between the known hosts and New Zealand native plants; 'Probability rank' rank of probabilities of sharing a herbivore species between known hosts and New Zealand native plants depending on their phylogenetic distance.

C.3 List of Coleoptera species in/ the GPDD database that might represent a threat for New Zealand native plants

Rank number	Pest name	Num. NZ potential hosts	Probability rank	Present in NZ	Same genus in NZ	NZ plants	Native range
1	*Diabrotica speciosa*	34	0.9546 – 0.1004				Neotropical
2	*Rhynchophorus ferrugineus*	10	0.9546 – 0.1179				Palearctic (Asia)
3	*Heteronychus arator*	12	0.9546 – 0.1183	Yes		Yes	Africa
4	*Rhynchophorus palmarum*	10	0.9546 – 0.1183				Neotropical
5	*Xenocompsa flavonitida*	5	0.9546 – 0.1263				Neotropical
6	*Euscepes postfasciatus*	4	0.9546 – 0.3158				-
7	*Micrapate scabrata*	16	0.9546 – 0.1004				Neotropical
8	*Diabrotica viridula*	15	0.9546 – 0.1279				Neotropical
9	*Odontota dorsalis*	5	0.9546 – 0.1092				Nearctic
10	*Lagria villosa*	2	0.9546				Afrotropical
11	*Atrachya menetriesi* *Aulacophora nigripennis*	2 2	0.9546 – 0.2599 0.9546 – 0.1541				- -
12	*Anomala cuprea* *Diabrotica emorsitans* *Diabrotica limitata* *Popillia japonica* *Epilachna vigintioctopunctata*	2 2 2 2 2	0.9546 – 0.1279 0.9546 – 0.1119 0.9546 – 0.1119 0.9546 – 0.1279 0.9546 – 0.1286	 Yes	 	 Yes	Palearctic (Japan) Neotropical Neotropical Palearctic (Asia) Palearctic (Asia)
13	*Agriotes sputator* *Epitrix aethiopica* *Henosepilachna elaterii* *Lagria cuprina* *Leptinotarsa decemlineata* *Melolontha melolontha* *Niphobleta niveosparsa* *Chelymorpha cribraria* *Orchestes fagi* *Otiorhynchus armadillo* *Euwallacea interjectus* *Agrilus hyperici* *Hylobius transversovittatus*	1 1 1 1 1 1 1 1 1 1 1 1 1	0.9546 0.9546 0.9546 0.9546 0.9546 0.9546 0.9546 0.9546 0.9546 0.9546 0.9546 0.9546 0.9546	 	 Yes 	 No 	Palearctic Afrotropical Palearctic - Nearctic Palearctic (Europe) - Neotropical Palearctic (Europe) Palearctic (Europe) Palearctic (Asia) Palearctic (Europe) Palearctic (Europe)
14	*Teratopactus nodicollis*	14	0.3720 – 0.1279				Neotropical
15	*Naupactus xanthographus*	6	0.3158 – 0.1263		Yes	Yes	Neotropical
16	*Oxythyrea funesta*	4	0.3158 – 0.2536				Palearctic
17	*Trogoderma granarium*	4	0.2356 – 0.1279				-
18	*Conotrachelus nenuphar* *Cyclocephala flavipennis*	2 2	0.2164 0.2164				Nearctic (North America) -
19	*Maladera castanea* *Batocera rubus*	1 1	0.2075 0.2075				Palearctic (Asia) Palearctic (Asia)
20	*Metamasius hemipterus sericeus*	5	0.2016 – 0.1183				Neotropical
21	*Rhabdoscelus obscurus* *Calyptocephala antennata* *Prosopodonta dorsata* *Metamasius hemipterus* *Brontispa longissima*	1 1 1 1 1	0.2016 0.2016 0.2016 0.2016 0.2016	 	 	 	Australasia (New Guinea) - Neotropical Neotropical Australasia
22	*Anoplophora maculata*	1	0.1663				Palearctic (Asia)
23	*Anomala cupripes*	6	0.1541 – 0.1183				Palearctic (Asia)
24	*Calloso bruchuschinensis*	2	0.1541 – 0.1279				Palearctic (Asia)
25	*Tychius cuprifer*	1	0.1541				Palearctic (Europe)
26	*Bruchus tristis* *Diabrotica nigropunctata* *Hypera postica* *Otiorhynchus ligustici* *Costelytra zealandica*	3 3 3 3 3	0.1527 0.1527 0.1527 0.1527 0.1527	 Yes	Yes Yes Yes	No No 	Palearctic - Palearctic (Europe) Palearctic Australasia (New Zealand)
27	*Euwallacea fornicatus*	5	0.1412 – 0.1092				-

28	*Coptocycla sordida*	1	0.1412				-
29	*Anomala expansa*	4	0.1279 – 0.1092				Palearctic (Taiwan)
30	*Lema bilineata*	1	0.1286		Yes	No	Neotropical
31	*Mesalcidodes trifidus*	1	0.1279	Yes	Yes	Yes	Palearctic (Asia)
	Acanthophorus serraticornis	1	0.1279				Palearctic (Asia)
	Dectes texanus	1	0.1279				Nearctic (North America)
	Epilachna varivestis	1	0.1279				Nearctic (North America)
	Rhyssomatus nigerrimus	1	0.1279				Nearctic (Mexico)
	Naupactus leucoloma	1	0.1279				Neotropical
	Acanthoscelides obvelatus	1	0.1279				Neotropical
	Adoretus sinicus	1	0.1279				Palearctic (Japan and
	Systates pollinosus	1	0.1279			X	Taiwan)
	Altica coerulea	1	0.1279				-
	Bruchidius atrolineatus	1	0.1279				-
	Callosobruchus analis	1	0.1279				Afrotropical
	Callosobruchus phaseoli	1	0.1279			No	Afrotropical
	Callosobruchus rhodesianus	1	0.1279				Afrotropical
							-
32	*Heilipus lauri*	1	0.1263				Nearctic (Mexico)
	Xyleborus glabratus	1	0.1263				Palearctic (Asia)
	Xylotrupes gideon	1	0.1263				Indomalayan and Australasia
33	*Exophthalmus similis*	8	0.1183 – 0.1005				Neotropical (Jamaica)
34	*Amasa truncata*	4	0.1183	Yes	Yes	Yes	Australasian (Australia)
	Chauliognathus lugubris	4	0.1183				Australasian (Australia)
	Paropsisterna beata	4	0.1183				Australasian (Australia)
	Phoracantha recurva	4	0.1183		Yes	No	Australasian (Australia)
	Phoracantha semipunctata	4	0.1183	Yes		No	Australasian (Australia)
	Myllocerus undatus	4	0.1183				Indomalayan (Sri Lanka)
	Conotrachelus copalensis	4	0.1183				Neotropical
	Conotrachelus psidii	4	0.1183				Neotropical
	Peltotrachelus cognatus	4	0.1183				-
	Xylotrupes siamensis	4	0.1183				Palearctic (Asia)
35	*Aeolesthes sarta*	5	0.1179 -0.1039				Palearctic (Asia)
36	*Agrilus planipennis*	1	0.1179				Palearctic (Asia)
	Pseudocneorhinus bifasciatus	1	0.1179				Palearctic (Japan)
37	*Exophthalmus vittatus*	4	0.1092 – 0.1005				Neotropical (Jamaica)
38	*Abyarachryson signaticolle*	3	0.1092				Neotropical (Chile)
	Adoretus tenuimaculatus	3	0.1092				Palearctic (Asia)
	Apriona japonica	3	0.1092				Palearctic (Asia)
39	*Octotoma scabripennis*	3	0.1087				Nearctic (North America)
	Sinoxylon conigerum	3	0.1087				-
40	*Scolytus intricatus*	1	0.1039		Yes	No	Palearctic

Table clarifications: being 'Num. NZ potential hosts' the number of plant genera that according to the phylogenetic distance between the known hosts and New Zealand native plants; 'Probability rank' rank of probabilities of sharing a pest species between known hosts and New Zealand native plants depending on their phylogenetic distance; 'Present in NZ' if the pest species is already present in New Zealand; 'Same genus in NZ' if the plant genus is already present in New Zealand; 'NZ plants' if they feed on native.

Appendix D

Invasive alien species' impact classification systems: a case study using expert elicitation

D.1 Literature review of existing impact assessments and impact classification system

D.1.1 Invasive alien species risk assessment and impact classification systems

Invasion ecology researchers and practitioners in governmental agencies from around the world have joined efforts over many years to develop comprehensive cost-effective strategies against invasive alien species (Essl et al. 2011; Nentwig et al. 2016). Prevention has been emphasized as the most cost-effective strategy, and risk assessment tools have a key role to identify potential future IAS (Essl et al. 2011). Generally, risk assessment is a structured process used to identify the potential IAS and therefore is part of the risk management process. Risk assessment attempts to predict the success of an introduced species or population at different stages of the invasion continuum (Kumschick and Richardson 2013).

In their review of risk assessments for biological invasions, Kumschick and Richardson (2013) pointed out that most risk assessments are taxon-specific, therefore plants, vertebrates and invertebrates are assessed separately. The reason is that authors assumed that invaders from the same taxon will share certain general traits, trait-combinations or trait-environment interactions. In contrast, some risk assessments are multi-taxon but ecosystem-specific, which mostly focus on aquatic systems. Others are both, taxon and ecosystem specific. For example, the Weed Risk Assessment model (WRA) of Pheloung et al. (1999) discriminates between weeds and non-weeds to help Australian regulatory authorities responsible for biosecurity. It was later applied in New Zealand, Hawaii, Chicago, the Czech Republic and Florida (Pheloung et al. 1999; Daehler et al. 2004; Jefferson et al. 2004; Krivanek and Pyšek, 2006; Gordon et al. 2008).

Risk assessment methods can be qualitative, semi-quantitative or quantitative. Fully qualitative or semi quantitative methods are generally based on expert knowledge. Most frequently they are semi-quantitative (e.g. Pheloung et al. 1999; ISPM 11; FAO 2004; Bomford, 2008) because they include some kind of impact assessment, which is usually qualitative.

D.1.2 Impact assessments

There are numerous impact assessment systems, which have been developed independently of any broader risk assessment methods. One of the first frameworks developed to assess ecological impacts of IAS was proposed by Parker et al. (1999), who argued that the total effect of an IAS included three dimensions: invasive range, abundance and local effects. Building on this approach, Goodell et al. (2000) highlighted that assessing local effects/**** is one of the greatest challenges for IAS ecological impact assessments because they depend on ecological interactions between invaders and the host communities or ecosystems, which are hard to measure. Goodell et al. (2000) defined local effects at five scales of ecological organization: Effects on species traits, such as poor growth; effects on genetic characteristics that can "pollute" native species populations by hybridization or introgression; influences on the abundance and dynamics of populations, commonly reducing population sizes or causing local extinctions; effects on communities through changes in native species richness or diversity; and effects on ecosystem processes such as nutrient cycling or disturbance regimes.

Based on Parker et al. (1999), Sandvik et al. (2013) developed an ecological impact assessment system where the impact of IAS is expressed along two axes, which are conceptually independent. One axis measures invasion potential, which replaces potential area colonised because this is typically unknown and increasing, and the second axis considers potential density and per capita effects as a measure of local ecological effect. The species' placement in the two-dimensional area is determined by a total of nine criteria that define the final impact category.

The three dimensions of Parker et al. (1999), previously noted, do not always form the basis of impact assessment systems. For example, they are not used by the on-line Bioinvasion Impact/Biopollution Assessment System (BINPAS 2010), which i/s a computerized quantitative system that considers the abundance and distribution of alien species to numerically express the magnitude of their impacts with a "Biopollution level" index (Narščius et al. 2012). This system has been applied to quantify and compare magnitudes of bio-invasion impacts in nine bioregions of the Baltic Sea, and it has been argued that it can also be used in other ecosystems (Zaiko et al. 2011). However, what the Sandvik et al. (2013) and BINPAS (2010) systems have in common is that they both base their assessment of impact only on ecological criteria, and socio-economic impacts are not considered.

Other rating systems tend to express IAS impacts primarily in terms of economic impacts because of the practicality of setting up priorities for research and control effort (Smallwood and Salmon 1992; Vilà et al. 2010). One of the first examples of IAS rating systems for natural ecosystems in economic terms was the system created by Smallwood and Salmon (1992), which was applied to rate the impacts of alien bird and mammal pests. In this case, the authors incorporated the rating system into the

framework of a quick-response strategy for evaluating and acting on the invasion of a potential ecological IAS. Following Smallwood and Salmon (1992), the SPS Agreement (WTO 1995) also proposed economic factors that must be considered when assessing the consequences of pest introduction or spread. Multiple methods of combining economic impacts are avaliable (ISPM 11; FAO 2004). Another approach was that taken by the Millennium Ecosystem Assessment framework (Millenium Ecosystem Assessment 2005), which linked ecological and economic impacts and assumed that ecological impacts influence ecosystem services (Vilà et al. 2009). However, rating systems that express IAS impacts just in economic terms, such as that proposed by Smallwood and Salomon (1992), frequently over emphasise impacts on agriculture over natural resources (Nentwig et al. 2010).

While there is an extensive literature on systems for assessing both risk and impact, there is little agreement on how impacts should be incorporated in the risk assessment and how impacts should be compared between invading taxa and ecosystems (Parker et al. 1999; Essl et al. 2011; Kumschick and Richardson 2013). Frequently, definitions of impact and the types of impacts included differ between systems, which creates inconsistencies when defining and quantifying impacts in invasion ecology (Kumschick and Richardson 2013). As previously noted, some systems focus on environmental/ecological impact, while others take into account some aspects of socio-economic impacts. Recently, however, there has been an increasing effort to create a standardized tool to quantify and compare impacts among taxonomic groups and geographic regions (Nentwig et al. 2016).

D.1.3 The generic impact scoring system

European scientists have been developing the 'generic impact scoring system' (GISS), which bases impact levels on published evidence rather than expert opinions (Nentwig et al. 2016). It was first developed by Nentwig et al. (2010) for alien mammals in Europe. To define different impact categories, the authors selected a list of "true alien" mammal species from the DAISIE database (Delivering Alien Invasive Species Inventories for Europe; www.europe-aliens.org), and conducted an extensive literature survey on their impacts. "True alien" species were those with a native distribution entirely outside of Europe that have established self-sustaining populations in Europe and were introduced before the year 1500. By comparing these invasive alien species' impacts, Nentwig et al. (2010) defined two impact classes, environmental and economic. Each class was subdivided into five categories. Environmental impacts were subdivided into competition, predation, hybridization, transmission of disease and herbivory. Economic impacts were subdivided into impacts on agriculture, livestock, forestry, human health and infrastructure. Impact values in each subcategory were ranked from zero to five, with zero meaning no detectable impact, and five being the highest impact possible in the region of interest. Nentwig et al. (2010) described each impact level in an attempt to make the scaling

process transparent and reproducible, while also allowing adaptations if new information became available.

When applied to alien birds in Europe, Kumschick and Nentwig (2010) found that both impact categories – environmental and economic – were very similar to those determined for mammalian invaders. However, one category per impact group was added because in some cases bird impacts were not considered in the study of mammalian invaders. "Impact on ecosystem" was added as a further mechanism of environmental impact, and "human social life disturbance" as a new sub-category accounting for economic impact. After this last modification, the GISS has been applied to alien fish (van der Veer and Nentwig 2014), terrestrial invertebrates (Vaes-Petignat and Nentwig 2014), aquatic invertebrates (Laverty et al. 2015), and plants (Novoa et al. 2016). Each additional taxon required further modifications (see Nentwig et al. 2016).

Here, I emphasise two adaptations of the GISS that I used in my own study. The first was made by Kumschick et al. (2012), who modified and applied the GISS for alien species prioritization. Kumschick et al. (2012) suggested a prioritization framework that included impact scoring and stakeholder opinions. A stakeholder was defined as a person who can affect or is affected by the issue at stake (Freeman, 1984, cited in Mitchell et al. 1997). Based on the GISS impact categories, they designed a complex five step species evaluation process involving scientists, stakeholders and decision makers whereby individual stakeholders were asked to weight some impact categories. Final scores were calculated from combining scientists' and stakeholders' values. In the case of IAS, stakeholders include agricultural and silvicultural producers, environmental organizations, tourist industry and representatives from municipalities (see details in Kumschick et al. 2012). However, stakeholders need to be selected first and ranked by decision makers in relation to the issue that is being evaluated, to form a stakeholder group sufficiently representative and appropriate for the task. By using this framework and accounting for positive and negative IAS effects separately, Kumschick et al. (2012) aimed to minimize conflicts arising from differing perspectives and biases of participants. Here, the terms "positive" and "negative" relate to the direction of environmental change relative to the pre-invasion state. Socio-economic changes, for example, can be negative or positive depending on whether they decrease or increase human well-being. Moreover, for each impact category, the confidence of the assessors' answers were assessed to evaluate the reliability of the data source used for scoring (low, medium, high). This confidence level was not integrated in the outcome of the impact scores, but was mentioned separately in the conclusions.

The second adaptation, made by Blackburn et al. (2014), aimed to align the GISS with the new impact scheme of the Global Invasive Species Database (GISD), which was implemented by the Species

Survival Commission (SSC) of the International Union for Conservation of Nature (IUCN) Red List categories and criteria. The Blackburn et al. (2014) classification was recently adopted as the official mechanism by the IUCN, seemingly after some corrections and clarifications were made by Hawkins et al. (2015). The classification was designed for use by scientists, land managers and conservation practitioners to better understand the magnitude of impacts caused by different taxa and to evaluate management policies and actions within existing international agreements and statues (Hawkins et al. 2015). In their classification, Blackburn et al. (2014) only considered deleterious environmental impacts, although they suggested it can also be applied to socio-economic impacts. In this case, the authors expanded the GISS by adding explicit scenarios from the GISD. These new mechanisms are parasitism, poisoning/toxicity, bio-fouling and interactions with other invasive species as new mechanisms of impact. These four mechanisms of impact were added to the six from the original classification, which were competition, predation, hybridisation, transmission of diseases, grazing/herbivory/browsing, and chemical, physical, or structural impact on ecosystems (Kumschick and Nentwig 2010; Blackburn et al. 2014). Moreover, Blackburn et al. (2014) established a new system to rank categories of impact. Each environmental mechanism was subdivided into five categories that qualitatively describe different degrees of impact. An extra subdivision was added for the category of unknown impact or insufficient evidence to assess it ('Data Deficient'). Unlike the original GISS for which only published information can be used for categorisation, Blackburn et al.'s (2014), categorisation of impact via each mechanism could be done using all available evidence of impact for the taxon in all regions where it has been introduced. The overall impact category of the species corresponded to the highest level of negative impact identified from any of the impact mechanisms. However, Blackburn et al.'s (2014) framework also captured the current impact level caused by that taxon at the same location or elsewhere in the geographical area of interest (Hawkins et al. 2015). According to Hawkins et al. (2015), parallel classifications of current and maximum impacts were intended to help indicate changes in current environmental impact through successive assessments. Blackburn et al. (2014) restricted analysis of uncertainty associated with impact scores to data reliability.

D.2 Questionnares to assess the IAS ecological impact and the linguistic uncertainty

	Ecological impact						Confidence score				Data reliability		
	Data Deficient (DD)	Minimal concern (MC)	Minor (MN)	Moderate (MO)	Major (MR)	Massive (MV)	Very confident (80-100%)	Somewhat confident (60-80%)	Neutral (40-60%)	Somewhat not confident (20-40%)	Low	Medium	High
Competition	○	○	○	○	○	○	○	○	○	○	○	○	○
Predation	○	○	○	○	○	○	○	○	○	○	○	○	○
Hybridisation	○	○	○	○	○	○	○	○	○	○	○	○	○
Transmission of diseases to native species	○	○	○	○	○	○	○	○	○	○	○	○	○
Parasitism	○	○	○	○	○	○	○	○	○	○	○	○	○
Poisoning/toxicity	○	○	○	○	○	○	○	○	○	○	○	○	○
Bio-fouling	○	○	○	○	○	○	○	○	○	○	○	○	○
Grazing/herbivory/browsing	○	○	○	○	○	○	○	○	○	○	○	○	○
Chemical, physical, or structural impact on ecosystems	○	○	○	○	○	○	○	○	○	○	○	○	○
Interaction with other alien species	○	○	○	○	○	○	○	○	○	○	○	○	○

Figure D.2.1 Questionnarie to assess the ecological impact of the species using the Blackburn et al. (2014) system

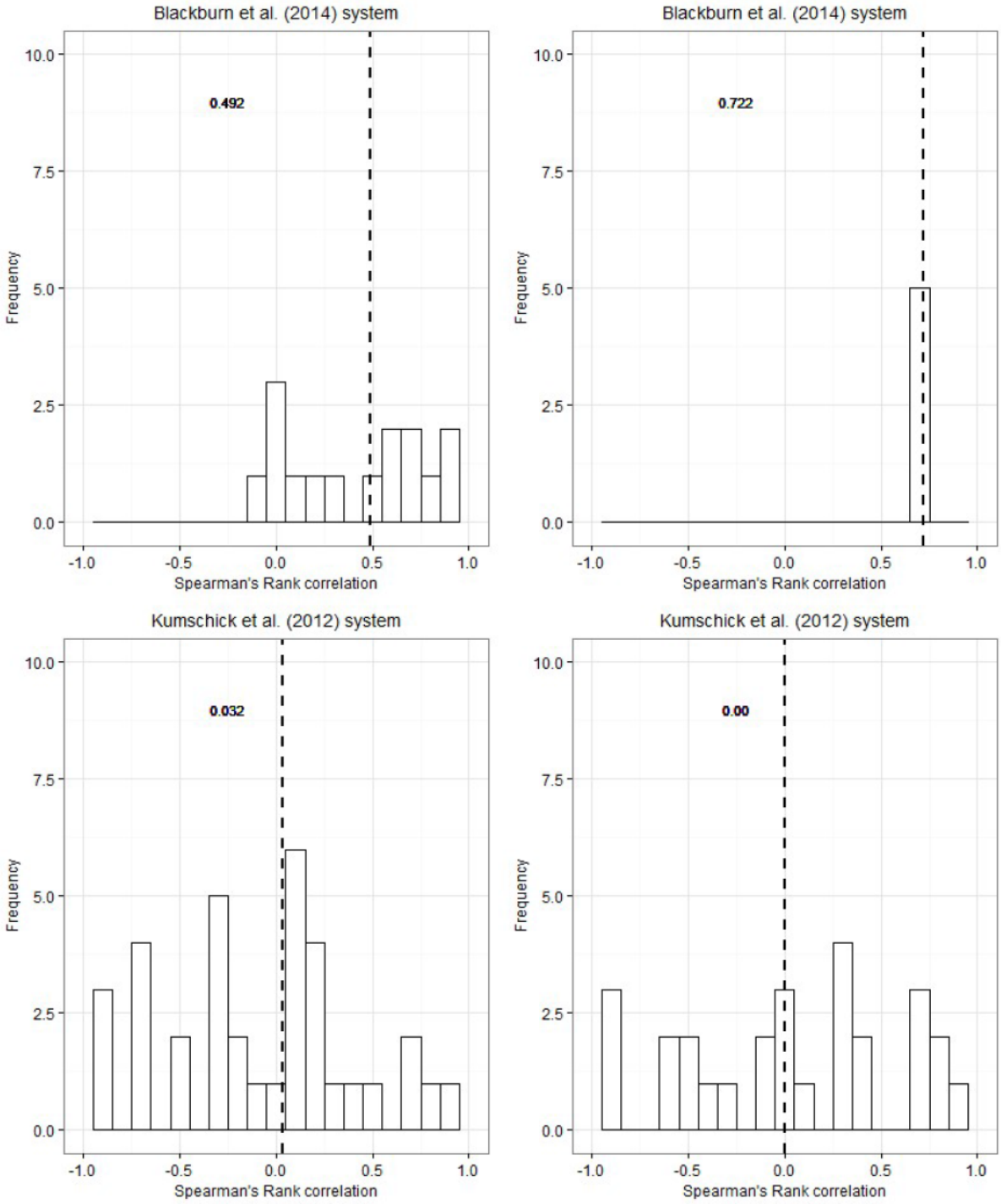
	Ecological impact						Confidence score				Data reliability		
	Score 0	Score 1	Score 2	Score 3	Score 4	Score 5	Very confident (80-100%)	Somewhat confident (60-80%)	Neutral (40-60%)	Somewhat not confident (20-40%)	Low	Medium	High
Herbivory/toxicity negative	○	○	○	○	○	○	○	○	○	○	○	○	○
Herbivory/toxicity positive	○	○	○	○	○	○	○	○	○	○	○	○	○
Competition negative	○	○	○	○	○	○	○	○	○	○	○	○	○
Competition positive	○	○	○	○	○	○	○	○	○	○	○	○	○
Predation negative	○	○	○	○	○	○	○	○	○	○	○	○	○
Predation positive	○	○	○	○	○	○	○	○	○	○	○	○	○
Transmission of diseases to wildlife negative	○	○	○	○	○	○	○	○	○	○	○	○	○
Transmission of diseases to wildlife positive	○	○	○	○	○	○	○	○	○	○	○	○	○
Hybridization negative	○	○	○	○	○	○	○	○	○	○	○	○	○
Hybridization positive	○	○	○	○	○	○	○	○	○	○	○	○	○
Impact on ecosystem negative	○	○	○	○	○	○	○	○	○	○	○	○	○
Impact on ecosystem positive	○	○	○	○	○	○	○	○	○	○	○	○	○

Figure D.2.2 Questionnarie to assess the ecological impact of the species using the Kumschick et al. (2012) system.

	Strongly agree	Agree	Neither agree nor disagree	Disagree	Strongly disagree
Were the questions clear?	O	O	O	O	O
Did you find that some of the questions were vague[1]?	O	O	O	O	O
Did you find the context specific[2] enough to understand the questions?	O	O	O	O	O
Did you find that the questions were ambiguous[3]?	O	O	O	O	O
Did you find some of questions' terms underespecific[4]?	O	O	O	O	O
Did you think there was indeterminacy in some of the theoretical terms used in the questions[5]?	O	O	O	O	O

Figure D.2.3 Assessment of the linguistic uncertainty (commune for both Blackburn et al. (2014) and Kumschick et al. (2012) systems).

D.3 Spearman's rank correlations between the ranks of the linguistic uncertainty related to the impact assessment methods of Kumschick et al. (2012) and Blackburn et al. (2014).



Values represent comparisons between pairs of participants within an impact classification system. Left figures represent the results of the first round of questionnaire responses, before discussions of the results and terms and concepts took place, while the right figures represent the results of the second round of impact evaluation and ranking after the discussions. Also, the figures showing inside each graph mean.

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